PROTOCYSTITES MENEVENSIS—
A STEM-GROUP CHORDATE (CORNUTA) FROM THE MIDDLE CAMBRIAN OF SOUTH WALES

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ABSTRACT. *Protocystites menevensis* Hicks, 1872, from the *Hypagnostus parvifrons* Zone of the Middle Cambrian, near St David's, Dyfed, South Wales, is reconstructed and redescribed. It proves to be a cornute, and therefore a stem-group chordate, representing a plesion intermediate between that of *Ceratocystis perneri* (the most primitive known chordate) and that of *Nevadaecystis americana*. For purposes of reconstruction, tectonic distortion of the fossils was corrected by means of a computer program. The positions of oesophagus, stomach, and intestine are suggested in *P. menevensis* on the basis of skeletal evidence. The locomotory cycle of the animal, which probably crept rearwards over the sea floor pulled by its tail, is deduced.

It is argued that, on a practical definition, every plesion is fundamentally paraphyletic. The term 'more crownward' is used to signify that a plesion is more closely related to the relevant crown group than is some other plesion. The term 'nodal group' is proposed for all those members of a group which possessed all the autapomorphies of the crown group but none of the autapomorphies of any of the subgroups of the crown group.

A comparison between stem chordates and the echinoderms shows that echinoderm 'dorsal' is homologous with chordate ventral and vice versa, so in echinoderms the use of the terms 'dorsal' and 'ventral' should be abandoned.

THE aims of this paper are to redescribe *Protocystites menevensis* Hicks, 1872, from the Middle Cambrian near St David's, Dyfed, Wales; to locate it stratigraphically; to reconstruct its skeletal anatomy, soft parts, and functional morphology; and to determine its systematic position. The species proves to be a stem-group chordate of the group Cornuta. It is the second most primitive cornute known and, at present, the oldest chordate known from Britain. Other interpretations regard *P. menevensis*, and all other cornutes, as echinoderms, e.g. Ubaghs (1967, 1981) and Philip (1979). One of us has argued elsewhere why these various views are mistaken and the arguments will not be repeated here (see Jefferies 1981*a*, *b*, 1986).

The present study of *P. menevensis* began in 1981 when the two junior authors independently examined the lectotype A.1021 in the Sedgwick Museum, Cambridge, and E432 in the British Museum (Natural History). They immediately recognized them as belonging to a species of cornute and several small expeditions to Porth-y-rhaw in 1982 to 1984 yielded much more material. The senior author devoted most of 1984 to reconstructing the animal in detail. The stratigraphical part of this paper results from the work of M. Lewis.

PHYLOGENETIC METHODOLOGY

The terms 'stem group' and 'crown group' as applied in this paper still require explanation (although their use seems to be spreading: Jefferies 1979; Patterson 1981; Smith 1984*a*; Paul and Smith 1984; Thulborn 1984). Given two sister groups (1 and 2) with still extant members (text-fig. 1), there are two obvious ways of delimiting both groups when extinct forms are taken into account. The narrower delimitation of group 2, for example, would include the latest common ancestor of all the living members, *plus* all its descendants, whether living or dead. This delimitation can be called the crown group as proposed in Jefferies (1979)—a term that corresponds to the *group of Hennig

(1969, 1981). The wider delimitation of group 2 would include all descendants of the latest common ancestor of groups 1 and 2 except members of group 1. This delimitation can be called the total group ('Gesamtgruppe' of Hennig). Now, if the crown group of 2 is subtracted from the total group of 2, a paraphyletic ancestral grouping remains which can be called the stem group of 2.

Within this stem group, it is theoretically important to distinguish the stem lineage of 2 (Ax, in press; 'Stammlinie' of Ax 1984)—this, for us, is the lineal sequence of ancestors and descendants which led from the latest common ancestor of [1 + 2] up to, but not including, the first member of crown group 2, which latter was the latest common ancestor of all living members of 2. (Our usage differs slightly from that of Ax, who includes the latest common ancestor of the living forms in the stem lineage as he defines it.) However, the stem group does not include the stem lineage alone: it also contains the 'side branches'—all descendants of the stem lineage which do not belong to the
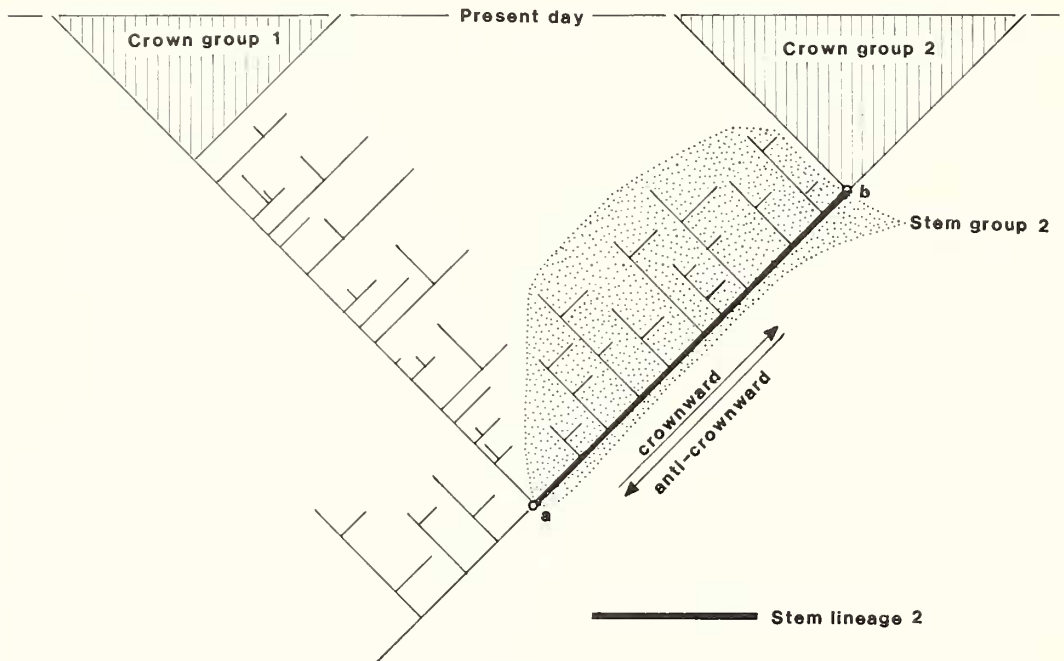
TEXT-FIG. 1. Stem group, crown group, and stem lineage. Crown groups 1 and 2 are sister groups with some members still living.

crown group. Within the stem group, it is possible to conceive of different degrees of relationship to the crown group, and Patterson and Rosen (1977, p. 165) proposed the term 'plesion' for 'fossil groups of species sequenced in a classification according to the convention that each such group is the plesiomorph sister-group of all those, living and fossil, that succeed it . . .'. By thus arranging plesions within the stem group in order of increasing relationship with the crown group, it is possible to reconstruct the sequence of origin of the autapomorphies of the crown group as these evolved within the stem lineage.

Patterson and Rosen implied, by using the term 'sister-group' in the definition quoted, that plesions are monophyletic. We should like to redefine the word 'plesion', however, to accord more with practical realities, as follows: a plesion includes all, and only, those members of a stem group which, so far as can be discerned, are equally closely related to the crown group. As discussed below, a plesion so defined, if fully known, is necessarily paraphyletic.
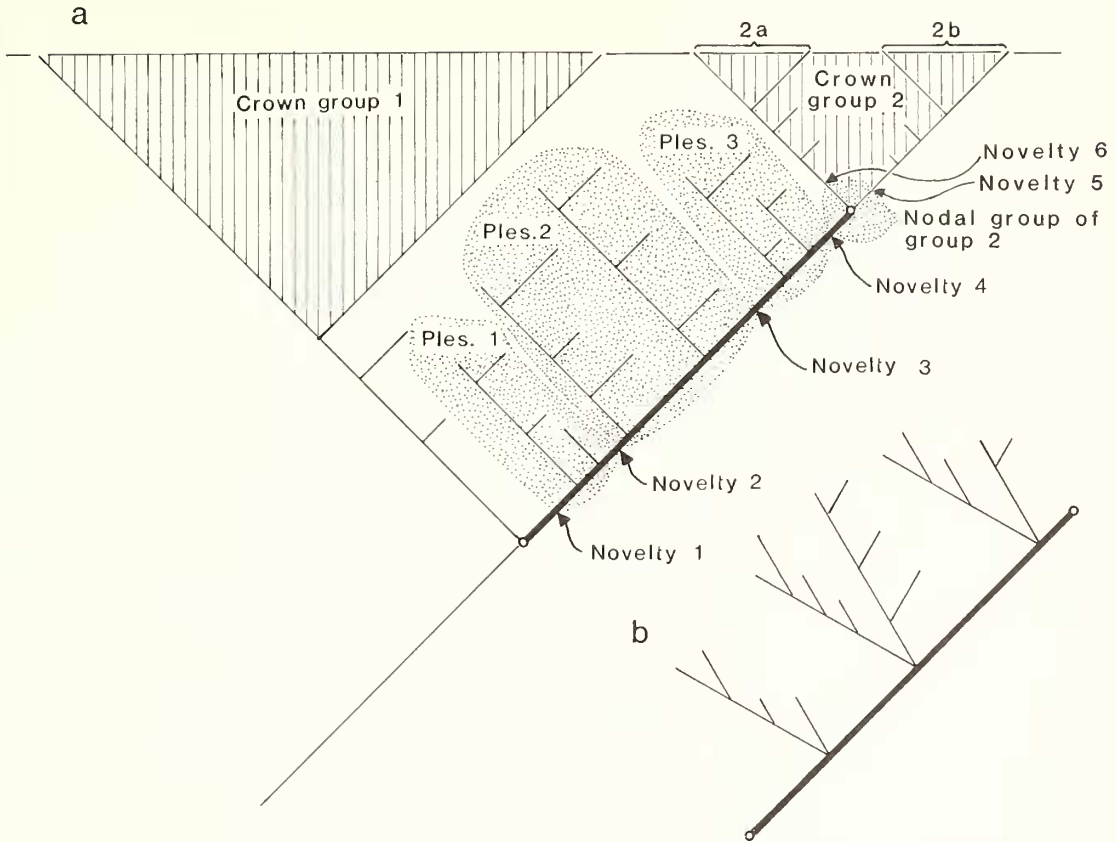
TEXT-FIG. 2. The paraphyletic nature of plesions and the position of the nodal group. *a*, the phylogeny of stem group 2 as it actually happened. *b*, cladograms of plesions 1, 2, and 3 so far as reconstructable.

The term 'crownward' has been proposed by Jefferies (1986, p. 13) to mean 'more closely related to the crown group'. Thus, within the stem group of group 2, plesion 3 (of text-fig. 2) is crownward of plesion 2. It is less ambiguous than 'higher', which may indicate stratigraphy, increase in complexity in any direction, or even moral approval; it is also clearer than 'more advanced' since it implies advance towards the crown group along the stem lineage only; and it is better than 'later' which ought to refer only to time. As opposite to crownward, we use 'less crownward' to signify position, or 'anti-crownward' to indicate direction.

To split a stem group into plesions we usually search for a feature shared with the crown group by some members of the stem group, but not by others. However, the feature sought need not be shared with all members of the crown group, since some may secondarily have lost it. And, indeed, a feature shared with more crownward plesions may be used, even when it was later lost within the stem lineage and is therefore primitively absent in the crown group itself. Thus the cornute *Nevadaecystis americana* (Ubaghs, 1963) possesses a strut, in common with more crownward plesions of the chordate stem group such as those of *Cothurnocystis elizae* Bather, 1913 and *Galliaecystis lignieresi* Ubaghs, 1969 (text-fig. 26), but unlike less crownward plesions such as those of *P. menevensis* and *Ceratocystis perneri* Jaeckel, 1900. The strut is a legitimate reason for putting the plesion of *N. americana* more crownward than that of *P. menevensis*. The strut is absent, however, from all mitrates, which are primitive members of the chordate crown group, and is

secondarily incomplete in the crownmost members of the chordate stem group, such as the cornute *Reticulocarpos hanusi* Jefferies and Prokop, 1972.

The plesion concept has some difficulties. When a palaeontologist begins to divide a stem group into plesions, each plesion will probably be monospecific, and therefore monophyletic as regards its only known constituent, and this monophyly accords with Patterson's and Rosen's concept of the term plesion. As study proceeds, however, this early false clarity will be lost, because more than one species will come to be assigned to each plesion, and often these species will not share synapomorphies with each other such as would show them to form, on their own, a monophyletic group. Indeed, the stem group can be divided into plesions only to the extent which changes in the stem lineage will allow. The smallest theoretically recognizable segment of a stem lineage will be the sequence of ancestors and descendants lying between one evolutionary novelty and the next more crownward one evolved in the stem lineage, e.g. the segment of the stem lineage within plesion 1, between novelties 1 and 2 in text-fig. 2. All side branches from this segment, together with the segment itself, will necessarily be members of the same plesion, in so far as this term is usable in practice. If, therefore, all members of such a plesion (all its constituent individuals) had come to be known, the plesion would include part of the stem lineage as well as any side branches. And this segment of the stem lineage would be ancestral to forms which did not belong to the plesion, i.e. to more crownward plesions and to the crown group itself. But such a fully known plesion would be paraphyletic by Hennig's definition of paraphyly since, being in part ancestral to non-members, it would have no ancestor common to it alone (Hennig 1966, p. 146). This would remain true, even if the relevant part of the stem lineage was only a single generation. As knowledge advances, therefore, a plesion will change from being monophyletic as regards its single known member species, to being possibly paraphyletic as regards all its known members. On the other hand, as soon as a formerly recognized plesion can be shown to be paraphyletic by demonstrating that an evolutionary novelty evolved within it in the stem lineage, then it will be split into two plesions, one of which will be more crownward than the other. The paradox is therefore reached that a plesion is by its nature paraphyletic, but as soon as it can be *shown* to be so in the particular case, it splits. Also it is possible to show that a particular fossil is *not* a member of the stem lineage if it possesses features which never existed in that lineage. But it is never, or almost never, possible to show that a fossil *was* a member of the stem lineage.

We use the term 'intermediate category' (Hennig's 'Zwischenkategorie') for an overtly paraphyletic grouping of two or more adjacent plesions within a stem group. Such provable paraphyletic groupings may sometimes be convenient to recognize. An example is the group Cornuta for the crownward part of the chordate stem group. (It is still unknown what fossils should be placed less crownward than the cornutes in the chordate stem group.)

We propose the term 'nodal group' for all those members of a monophyletic group which possess all the autapomorphies of the crown group, but are primarily lacking any of the autapomorphies of any of the subgroups of the crown group. Thus, with reference to group 2 in text-fig. 2, the nodal group will show novelty 4 (the last one evolved in the stem lineage of group 2) but will lack novelties 5 and 6 (the first ones evolved in the respective stem lineages of the major subgroups of 2, i.e. 2a and 2b). Thus the nodal group will include the latest common ancestor of the extant members of group 2, and this gives it particular importance, but it will also contain the most crownward parts of the stem group of 2 and the least crownward parts of the stem groups of subgroups 2a and 2b.

The word 'calcichordate' was proposed by one of us (Jefferies 1967) for any chordate with a calcite skeleton of echinoderm type, and in particular for the cornutes and the mitrates. On these definitions, *P. menevensis* is a calcichordate. However, in the light of Hennig's work (1969, 1981) the 'Calcichordata' form an 'invalid stem group' since the cornutes are stem-group chordates while the mitrates are primitive crown-group chordates (Jefferies 1979, 1986). Consequently, the word 'calcichordate' is best abandoned or, at most, used informally. The word 'Stylophora' (Gill and Caster 1960) is coextensive in meaning with Calcichordata. It should be abandoned for the same reasons, and also because the workers who use it mistakenly regard the cornutes and mitrates as echinoderms and it wrongly implies that the cornute stylocone is homologous with the mitrate styloid.

METHODS OF STUDY

P. menevensis was reconstructed by one of us (R.P.S.J.) on a drawing board, several projections being plotted simultaneously as with previous such studies (e.g. Jefferies 1968, 1969). The specimens were examined by means of latex casts to reconstruct the skeleton, and by direct observation of internal moulds to reconstruct the soft parts. Sometimes pyrite and limonite were removed from the fossils by soaking them overnight in 10% thioglycollic acid; this cleaning allowed much better latex casts to be made.

Correction of distortion

Tectonic distortion made great difficulties. These were partly overcome by means of a computer-graphical method based on suggestions by Appleby and Jones (1976) and Ramsay (1967). The bedding planes of the shale in which the specimens occur are crossed by stretching lineations which give the rock a slight graininess like that of wood. All these lineations run parallel to tight parallel folds in the thinner shelled trilobites and represent the long axis (*x*-axis) of the strain ellipse for the bedding plane; the direction at right angles to them (*y*-axis) is the direction of greatest compression in the bedding plane. The original outline of a plate would therefore correspond to the observed outline expanded by some definite factor along the *y*-axis, perpendicular to the lineations.
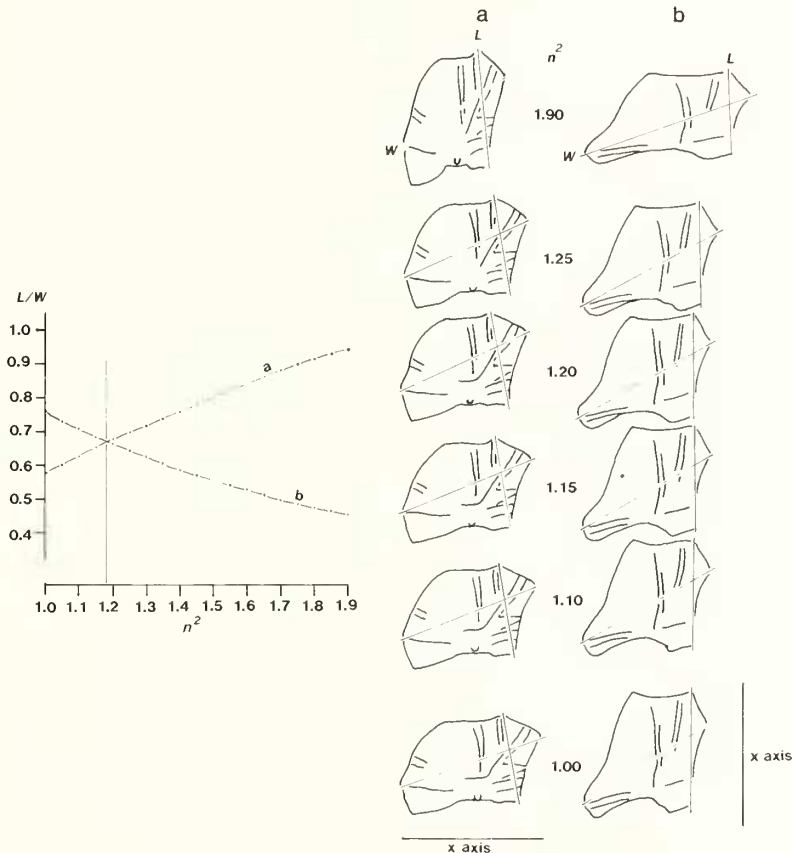
TEXT-FIG. 3. Correction of distortion on the basis of two specimens of *P. menevensis* Hicks plate g (see text-fig. 10) compressed approximately perpendicular to each other. The *x*-axis is the presumed major axis of the strain ellipse. Specimen *a*, BM(NH) E62952; specimen *b*, BM(NH) E62930; n^2, proportionate increase of unit length along the *y*-axis, relative to the *x*-axis (further explanation in text).
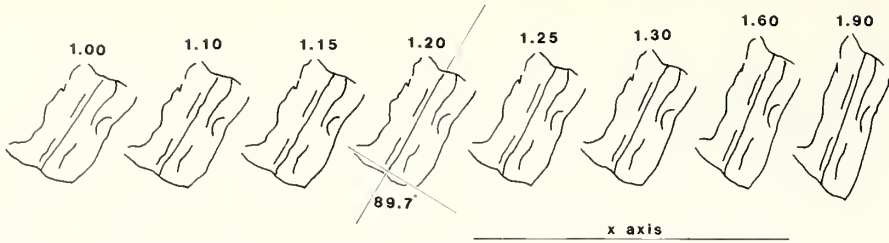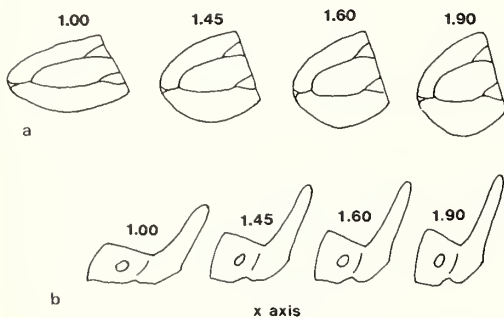
TEXT-FIG. 4. Correction of distortion of a hind-tail ossicle of *P. menevensis* Hicks, BM(NH) E432. The numbers show n^2 (see text).

A computer program was devised by Mr A. J. Paterson of the Biometrics Section, British Museum (Natural History), to modify the observed outlines in the manner required. To use this program, camera-lucida drawings of the specimen were placed on a digitizer with the x-axis (assumed to be parallel to the stretching lineations) arranged parallel to the x-axis of the digitizer. The shape in the drawing was transformed into x–y coordinates by tracing the outline with the cross-wires on the 'puck' (follower) of the digitizer. The y coordinates were then multiplied by a factor n, while the corresponding x coordinates were multiplied by $1/n$. The results of these multiplications were displayed on a visual display unit and simultaneously drawn, as needed, on a plotter. It was also possible to multiply both sets of coordinates by a uniform factor M so that the visual output was magnified to a convenient size. The proportionate increase of the y coordinate relative to the x coordinate was n^2 (since $n \div (1/n) = n^2$).

To decide the appropriate value of n^2, and therefore n, was not easy. With initially symmetrical structures, such as the obliquely distorted heads or tails of trilobites or the tail ossicles of *Protocystites*, the presumed correct value restored the initial symmetry. With asymmetrical structures, such as the head plates of *Protocystites*, it was necessary to find two specimens of the same plate compressed in different directions, preferably at right angles. The appropriate value of n^2 would then be the one that gave the same shape to the two specimens. In fact, this ideal agreement was never achieved, and it was therefore necessary to use some index of shape, such as the ratio of the length of two chosen lines on the plates or the angle of some prominent corner. The appropriate value of n^2 was then the one that gave identical values for the index.

When comparing two specimens of corresponding plates compressed in different directions, a series of computer plots was made for both plates with n^2 increasing at increments of 0·05 from 1·05 to 1·70. Graphs were then drawn of n^2 against the measured value for the chosen index for both plates. The appropriate value of n^2 was that at which the indexes of both plates were equal, i.e. where the lines for the two plates crossed each other on the graph. At this value, the computer plot was presumed to show the original shape of the plate.

The deduced values for n^2 are not uniform. Three head plates (e, g, and k on text-fig. 10) gave values of n^2 close to 1·20 (text-fig. 3). The same value was found to hold for an isolated hind-tail ossicle (text-fig. 4) and for the hind-tail ossicles of the lectotype (designated below). On the other hand, two specimens of the left

TEXT-FIG. 5. Correction of distortion for two trilobite cephalons. a, *Ptychagnostus*. b, *Eodiscus*. The numbers show n^2 (see text).

process (the process on plate 1), which was thin and is sometimes visibly crumpled, required a higher value of n^2 at about 1·60. The same value was required to restore symmetry to the trilobite *Eodiscus* (text-fig. 5*b*) whereas a specimen of the cephalon of *Ptychagnostus* (text-fig. 5*a*) became symmetrical at about $n^2 = 1·15$. The highest values of n^2, as shown by the trilobite *Eodiscus*, probably approach the distortion of the matrix itself, whereas the lower values usually shown by the skeleton of *Protocystites menevensis* suggest that stereom calcite or its pyritic replacement was, because of its strength, less distorted than the surrounding rock. Indeed many specimens of *P. menevensis* seem to have responded to tectonic pressure by the plates sliding over or against each other, as well as by changing their outline. Sometimes adjacent tail ossicles have been pushed against each other, causing very high local pressures and non-homogeneous distortion, as testified by highly asymmetrical outlines. It is impossible to make proper allowance for these variations.

The reconstructions are therefore based on computer plots with $n^2 = 1·20$ ($n = 1·095$) which seems to be correct for the tougher parts of the head and tail skeleton of *P. menevensis* (cf. text-fig. 6). The results are probably better than those that would be obtained using uncorrected drawings of the specimens. Nevertheless, there is uncertainty about the shapes of the plates and the relative sizes of different parts of the animal, and this must be remembered in considering the reconstructions.
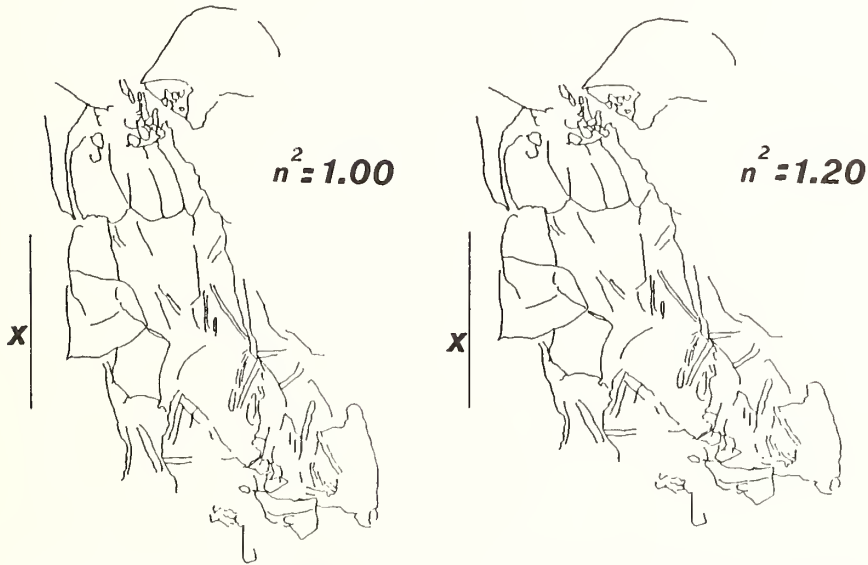
TEXT-FIG. 6. *Protocystites menevensis* Hicks; uncorrected and corrected drawings of BM(NH) E62963 (ventral aspect). The numbers show n^2 (see text).

Distortion perpendicular to the bedding planes is an even bigger problem than distortion in the plane of bedding. Thin parts of the skeleton, which originally stood almost vertical, and thus perpendicular to the bedding plane, have sometimes been squashed flat on to the bedding plane. This is particularly true of the posterior wall of the head in plates f, g, j, and k (see text-fig. 10). To obtain some idea of the original shape of these plates, replicas based on computer plots with $n^2 = 1·20$ were cut in aluminium sheet and bent to the likely original shape in three dimensions. Once again, the results are uncertain, so that the vertical dimension of the reconstructions is not reliable.

Tectonic distortion can thus be partly, but not totally, corrected; better reconstructions will require undistorted material (which may never be found). It is remarkable that tectonic distortion has not destroyed the histology of the plates, for the superficial features of different types of stereom can readily be recognized. (The three-dimensional structure of the stereom is not usually deducible.)

SYSTEMATIC PALAEONTOLOGY

Superphylum DEUTEROSTOMIA Grobben, 1908
Subsuperphylum DEXIOTHETICA Jefferies, 1979
Phylum CHORDATA Bateson, 1886
[Stem group of the Chordata]
Intermediate category CORNUTA Jaekel, 1901
Plesion of *Protocystites menevensis* herein
Genus PROTOCYSTITES Hicks, 1872

Type species. *P. menevensis* Hicks, 1872, by monotypy.

Systematic position. The above statement of systematic position is unorthodox. We deliberately have not placed *P. menevensis* in a family because it is at present alone in its plesion. Any family which included it, therefore, would either be: 1, coextensive with the species *P. menevensis* and therefore redundant; or 2, it would include one or more of the adjacent plesions of the chordate stem group—it would thus be overtly paraphyletic and (unlike the overtly paraphyletic grouping Cornuta, for example) would, in our opinion, never be a useful grouping in practice. Another unorthodoxy is that the intermediate category Cornuta is here given no conventional Linnaean rank. This omission is likewise deliberate and is based on the fact that nobody has yet explained how Linnaean rank can objectively be assigned, particularly to paraphyletic groupings of fossils (Ax, 1984, Ch. K; Ax, in press). Those ranks which are assigned above are either hallowed, though not validated, by long usage (superphylum, phylum) or else are obtained by interpolation (subsuperphylum).

Protocystites menevensis Hicks, 1872

Plates 54–60; text-figs. 6, 10, 15–19, 23–25

1866 *Protocystites* Salter *in* Hicks and Salter, p. 285 (*nom. nud.*).
1871 *Protocystites menevensis* Hicks *in* Harkness and Hicks, p. 396 (*nom. nud.*).
1872 *Protocystites menevensis* Hicks, pl. 5, fig. 19; p. 180 (lower illustration only).
1873 *Protocystites menevensis* Hicks; Salter, p. 3.
1887 *Protocystites meneviensis* Hicks; Barrande, p. 10.
1900 *Protocystis* Hicks; Bather, p. 48.
1943 *Protocystites meneviensis* Hicks; Bassler and Moody, p. 184.
1967 *Protocystites* Hicks; Ubaghs, p. S493.
1967 *Protocystites meneviensis* Hicks; Paul *in* Jefferies *et al.*, p. 567.
1979 *Protocystites meneviensis* Hicks; Paul, p. 453.

Comments on synonymy. The only previous figure and description of *Protocystites menevensis* was that of Hicks (1872). His illustration shows two specimens which can be identified with specimens A.1021 and A.1022 now held in the Sedgwick Museum, Cambridge. Of these, A.1022 is the operculum of a hyolithid, whereas A.1021 is a fairly good specimen of the species described in this paper and is here designated as lectotype (text-figs. 17 and 18; Pl. 56, figs. 1–3; Pl. 57, figs. 1 and 2). Hicks's figure is very poor and the species is not recognizable from it. Subsequent references to the species or genus, therefore, add nothing to knowledge and are of purely bibliographic interest.

The name *Protocystites* must not be confused with *Proteocystites* Barrande, 1887 which is a diplorite cystoid (see e.g. Kesling 1967, p. S248) and an echinoderm.

Material, horizon, and locality. The material examined is as follows:

(*a*) Sedgwick Museum, Cambridge: A.1021 (here chosen as lectotype) *ex* Hicks Collection, locality Porth-y-rhaw near St David's, Dyfed, horizon Menevian. Figured by Hicks (1872, pl. 5, fig. 19, lower figured specimen only) (text-figs. 17 and 18; Pl. 56, figs. 1–3; Pl. 57, figs. 1 and 2).

(*b*) British Museum (Natural History), London: i, old material, E432 *ex* Hicks Collection, locality St David's, horizon Menevian (text-fig. 19; Pl. 58, fig. 1); ii, new material, E62912–E62921, E62923–E62925, all from loc. 1, Porth-y-rhaw (text-figs. 7 and 8), horizon middle part of *Hypagnostus parvifrons* Zone, Middle Menevian; iii, also new material, E62926–E62934, E62937–E62939, E62942–E62945, E62950, E62952, E62955–E62966, E62968–E62981, E63006–E63056, all from loc. 2, Porth-y-rhaw (text-fig. 7), horizon nearly or exactly the same as for loc. 1.
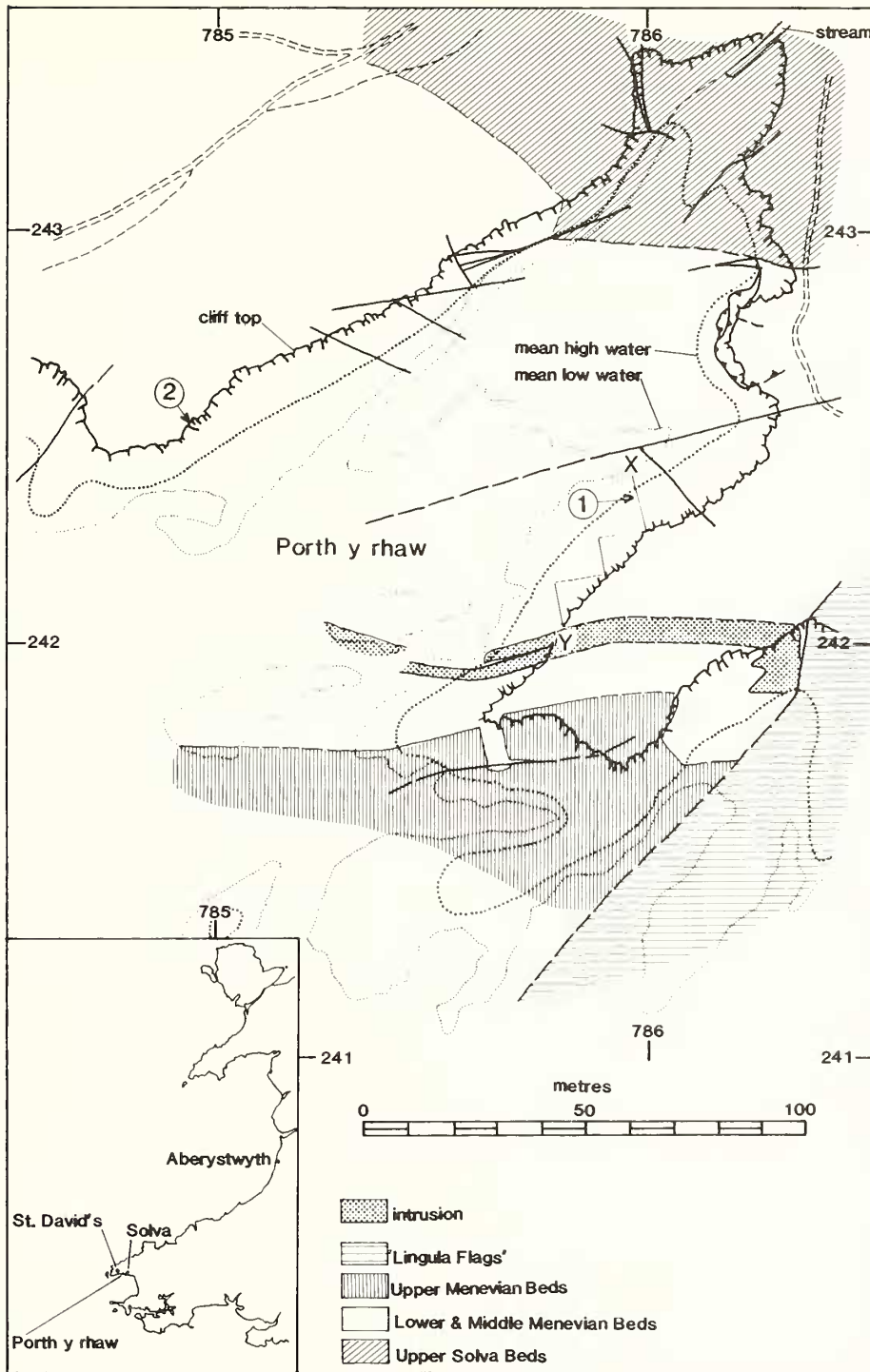
TEXT-FIG. 7. Geology and topography of Porth-y-rhaw, Dyfed, Wales. 1 and 2 are the localities that produced the new material of *Protocystites menevensis* Hicks. X and Y are respectively the lower and upper ends of the composite profile shown in text-fig. 8.

(c) National Museum of Wales, Cardiff: NMW.80.34G.948–958, all from loc. 1, Porth-y-rhaw, same horizon as BM(NH) material from that locality.

Most of the material consists of dissociated plates. All of it is tectonically distorted. Articulated specimens include SM A.1021 (lectotype) and BM(NH) E432, E62950, E62952, E62963 (the most instructive specimen; text-figs. 6, 15, 16; Pl. 54, figs. 1–3; Pl. 55, figs. 1 and 2), E62977, E62979.

Porth-y-rhaw, from which all the recently found material came (our locs. 1 and 2; text-figs. 7 and 8) (as also did one, or perhaps both, of the two nineteenth-century specimens), is a small inlet situated on the coast of Dyfed, Wales, about 3·6 km east-south-east of the cathedral of St David's and about 1·5 km west of Solva Harbour (text-fig. 7). The east side of Porth-y-rhaw (including our loc. 1) is the type section (text-fig. 8) of the Menevian Group of Hicks and Salter (1866). It was on this eastern side that Salter discovered *Paradoxides davidis* Salter, 1863 and its associated fauna in 1862, by chance, as a result of misnavigation. Text-fig. 9 shows the now accepted stratigraphical divisions for the Middle Cambrian near St David's.

Loc. 1 is on the eastern cliff section, Porth-y-rhaw (NGR SM 78596 24235), middle part of *H. parvifrons* Zone, at shore level, stratigraphically *c.* 22–24 m below the basal contact of two, almost vertical, 4 m thick sills and approximately 10–12 m stratigraphically below the local base of the *Ptychagnostus punctuosus* Zone (text-figs. 7 and 8). The nature and distribution of the fauna is shown in text-fig. 8.
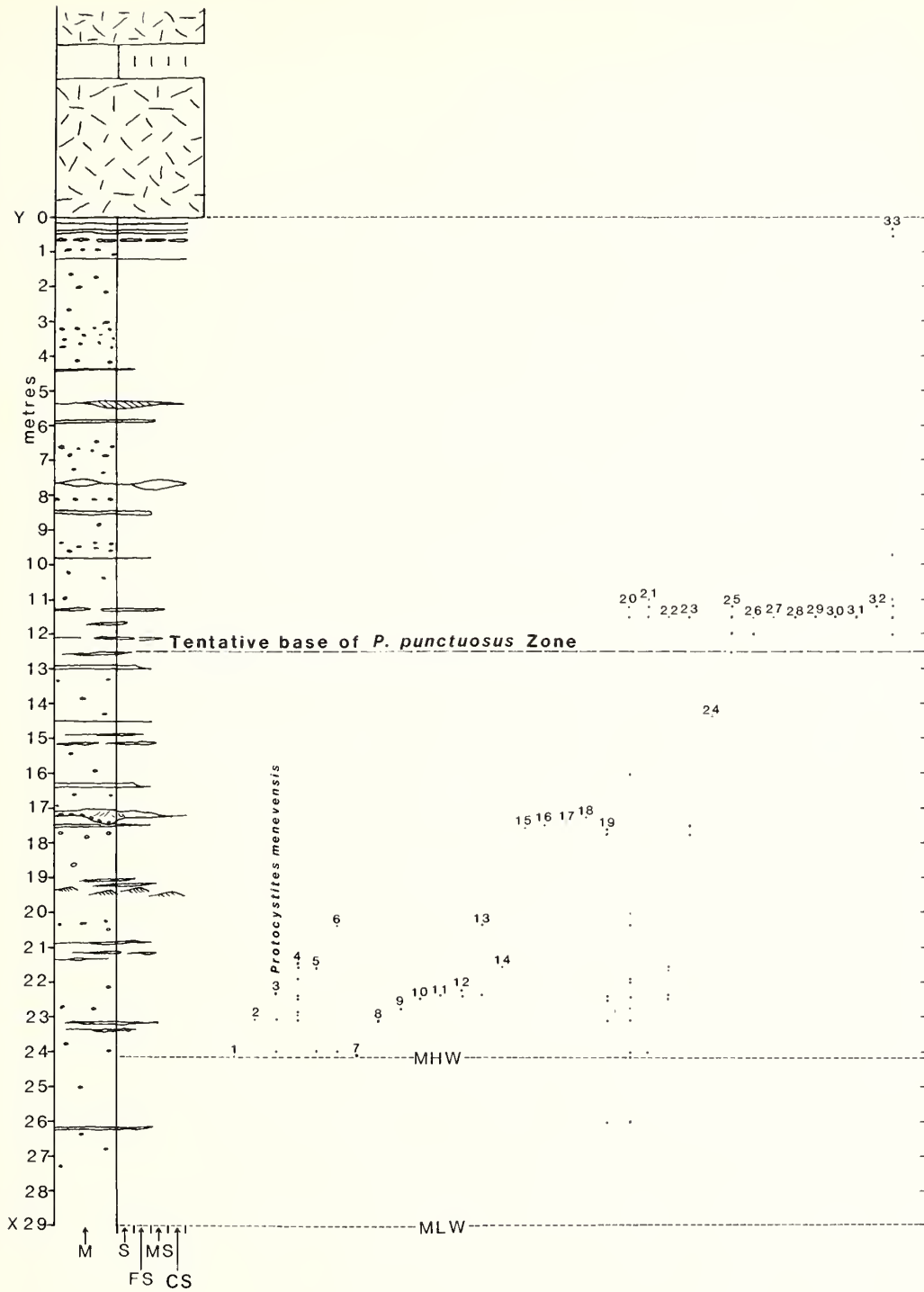
Loc. 2 (text-fig. 7) is on the western cliff section, also in the *H. parvifrons* Zone at or near the same horizon as loc. 1, just above the cliff top near the southern end of Porth-y-rhaw (NGR SM 78492 24252). Here the beds are less cleaved and more suitably weathered for yielding fossils than at loc. 1. In addition to *Protocystites menevensis*, the fauna here comprises the trilobites *Ptychagnostus ciceroides* (Matthew, 1896), *P. davidis* (Hicks, 1872), *P. punctuosus affinis* (Brögger, 1878), *P. punctuosus* s.l. (Angelin, 1851), *Cotalagnostus lens* (Grönwall, 1902), *Phalacroma bibullatum* (Barrande, 1846), *Peronopsis scutalis scutalis* (Hicks, 1872), *P. fallax depressa* Westergård, 1946, *Phalagnostus* cf. *nudus* (Beyrich, 1845), *Eodiscus punctatus punctatus* (Salter, 1864), *Agraulos longicephalus* (Hicks, 1872), *Jincella applanata* (Hicks, 1872), *Hartshillina spinata* (Illing, 1916), *Clarella salteri* (Hicks *in* Salter, 1865), *Acontheus* n. sp. aff. *A. inarmatus* Hutchinson, 1962, and a pagetiid (new genus); and the non-trilobite fossils *Linnarssonia sagittalis* (Davidson, 1871), *Lingulella* sp., *Hyolithes corrugatus* (Salter, 1864), *Stenotheca cornucopia* Hicks, 1872, *Protospongia fenestrata* Salter, 1864, and *Ctenocystis* sp. The record of *Ctenocystis* sp. is of interest as being the only known occurrence of the genus in Britain.

In the western cliff section, where loc. 2 is situated, the stratigraphically overlying *punctuosus* Zone seems to be unrepresented and the base of the *parvifrons* Zone could not be located exactly. However, evidence of the underlying *Tomagnostus fissus–Ptychagnostus atavus* Zone was found 40 m stratigraphically below loc. 2. As already stated, some 12 m of the *parvifrons* Zone exists in the eastern cliff section above the horizon of loc. 1 (text-fig. 8). If the horizons of locs. 1 and 2 are identical, therefore, the greatest possible thickness of the *parvifrons* Zone at Porth-y-rhaw is 12 + 40 = *c.* 52 m.

In biostratigraphic terms, 'Menevian' (text-fig. 9) conventionally refers to the traditional zones of *Paradoxides hicksii* and *P. davidis* and possibly other zones. References covering the most important faunas in the Menevian Group include Salter (1863, 1864, 1865), Salter and Hicks (1867, 1869), Hicks *in* Harkness and Hicks (1871), and Hicks and Jones (1872). Most of the trilobites were redescribed by Lake (1906–1946) and they indicate the presence of the *fissus*, *parvifrons*, and *punctuosus* zones of Scandinavian terminology.

The term 'Lower Menevian' is equivalent to the *hicksii* Zone of authors, which can be equated approximately with the *fissus–atavus* Zone of Sweden. *P. hicksii* is here considered a probable senior subjective synonym of

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TEXT-FIG. 8. Stratigraphic log of the beds exposed on the foreshore on the eastern side of Porth-y-rhaw, between points X and Y of text-fig. 7, and a complete list of the fossils found in that section. The profile is a composite, built up from three separate sections as shown in text-fig. 7. Locality 1 is at 22–24 m below the lower dolerite sill and is just above mean high-water mark. Abbreviations: M, mud; S, silt; FS, fine sand; MS, medium sand; CS, coarse sand; MHW, mean high water; MLW, mean low water; 1, *Hyolithes* sp.; 2, *Ptychagnostus punctuosus affinis*; 3, *Protocystites menevensis*; 4, pagetiid gen. et sp. nov.; 5, *Linnarssonia sagittalis*; 6, centropleurine fragments; 7, *Meneviella* sp. indet.; 8, *Ptychagnostus punctuosus* s.l.; 9, *Acontheus* sp. nov.; 10, *P. davidis*; 11, *H. corrugatus*; 12, *Jincella applanata*; 13, *Peronopsis fallax depressa*; 14, *Protospongia* sp.; 15, conocoryphid gen. et sp. indet.; 16, *Peronopsis* sp.; 17, *M.* cf. *venulosa*; 18, '*Leperditia*' *hicksi*; 19, *P. scutalis scutalis*; 20, *Eodiscus punctatus punctatus*; 21, *Cotalagnostus lens* (s.l.); 22, *Ptychagnostus ciceroides*; 23, *M. venulosa*; 24, *Clarella* sp.; 25, *P. punctuosus punctuosus*; 26, *Anopolenus henrici*; 27, *Peronopsis* ex gr. *fallax*; 28, *Pleuroctenium* cf. *bifurcatum*; 29, *Holocephalina* cf. *primordialis*; 30, *Phalagnostus* cf. *nudus*; 31, *Solenopleurina variolaris*; 32, *Pseudoperonopsis* sp.; 33, *Paradoxides davidis*.

ST. DAVID'S SERIES

Lejopyge laevigata	U.	MENEVIAN 'GROUP'
Solenopleura brachymetopa	?	
Triplagnostus lundgreni & Goniagnostus nathorsti		
Ptychagnostus punctuosus (Paradoxides davidis)	M.	
Hypagnostus parvifrons		
Tomagnostus fissus & Ptychagnostus atavus (Paradoxides hicksii)	L.	
	U.	SOLVA 'GROUP'
Ptychagnostus gibbus	M.	
Paradoxides harknessi	L.	
		CAERFAI 'GROUP'

TEXT-FIG. 9. Stratigraphical subdivisions of the Middle Cambrian of St David's (modified after Cowie *et al.* 1972). The zones of *Paradoxides hicksii* and *P. davidis* are traditional for the South Welsh area; those shown to their right are the equivalent zones of the Scandinavian succession. The traditional zones are shown here with their traditional extent, although *P. davidis* at Porth-y-rhaw is in fact unknown outside the *Ptychagnostus punctuosus* Zone.

P. aurora Salter *in* Salter and Hicks (1869), and its range is extended downwards to the base of the Upper Solva Beds. The Lower Menevian Beds, estimated by Hicks (1881, p. 299) to be 300 ft (91 m) thick, consist of light-grey and dark-grey laminated mudstones which suffered soft sediment deformation in the lower part. Towards the top of the division are some greenish mudstone units, lithologically similar to the Upper Caered Mudstones (Nicholas 1916) of St Tudwal's Peninsula, North Wales.

The Middle Menevian Beds were estimated by Hicks (1881, p. 299) and by Stead and Williams (1971, p. 181) to be 350 ft (107 m) thick, although a precise boundary between these and the Lower Menevian Beds was not defined by these authors. The Middle Menevian Beds are darker and more uniform in colour than the Lower Menevian Beds and consist of cleaved pyritic mudstones with occasional thin, sometimes lenticular, sandy horizons and several thin ($<$ 10 cm) pale beds which, according to Nicholas (1916, p. 99) are composed of ashy material. Certain beds contain numerous small flattened phosphatic nodules, and these and the Lower Menevian strata appear to have been deposited in a euxinic environment (Rushton 1974, p. 90). In biostratigraphic terms 'Middle Menevian' is equivalent to the *davidis* Zone of certain authors, which corresponds approximately to the *parvifrons* and *punctuosus* zones of Scandinavian nomenclature (text-fig. 9). The species *P. davidis*, however, seems at Porth-y-rhaw to be confined to the *punctuosus* Zone.

The Upper Menevian Beds at Porth-y-rhaw abruptly succeed the Middle Menevian beds and comprise coarse, dark-grey sandstones with shaly interbeds. These sandstones, exposed at the tip of the eastern headland of Porth-y-rhaw (text-fig. 7), are massive. They form beds up to 1 m thick at the base of the unit and seem to mark the initiation of deposition from current-agitated water or from turbidity currents. This style of deposition continued into '*Lingula* Flags' times (Rushton 1974, p. 90).

The Upper Menevian Beds of Porth-y-rhaw were said to be 100 ft (30 m) thick by Hicks (1881, p. 299) and Stead and Williams (1971, p. 81) but these authors did not define an upper limit. The sandstones contain '*Billingsella*' *hicksi* (Davidson) and other brachiopods and are commonly referred to as '*Orthis*' *hicksi* Beds.

Hicks (1892, p. 22) collected *Paradoxides* and a new species of '*Conocoryphe*' from them. These identifications suggest that the Upper Menevian of this locality may partly correspond to the *P. forchhammeri* 'Stage' of the Scandinavian sequence.

Stead and Williams (1971, p. 188) believed that the junction between Middle and Upper Menevian beds was conformable. However, Taylor and Rushton (1972, p. 9) suggested a widespread non-sequence at this level in England, Wales, and south-eastern Newfoundland caused by a regression during the time of the *Solenopleura brachymetopa* Zone.

As to correlation, the beds of the *parvifrons* Zone are correlated with: the upper part of the Nant-pig Mudstones of St Tudwal's Peninsula, North Wales (Rushton 1974, p. 72; after Nicholas 1916); Illing's (1916) horizons F1–F3, representing the *parvifrons* Zone in the Abbey Shales of Warwickshire (Rushton 1979, p. 43); beds in the lower part of the Clogau Formation in the Harlech Dome, North Wales (Allen *et al*. 1981, p. 303); the lower part of the *davidis* Zone in the Manuels River Formation, south-eastern Newfoundland (Hutchinson 1962); and the *parvifrons* Zone of Scandinavia (summarized by Martinsson 1974). Thomas *et al*. (1984, p. 888) discussed the distribution of the various trilobite species in these rocks.

The lithostratigraphical terminology used for the rocks of Porth-y-rhaw in this paper is in need of revision, but it is not appropriate to make this revision here.

Thus the total stratigraphical range of *Protocystites menevensis* is not known, although all of the abundant new material comes from the middle part of the *parvifrons* Zone of the Middle Menevian. The horizon of the lectotype cannot be ascertained exactly, beyond the fact that it came from the Menevian of Porth-y-rhaw. Harkness and Hicks (1871, p. 396) recorded the species from both Lower and Middle Menevian Beds but this does not tally with our experience.

Preservation and conditions of deposition. The plates of *P. menevensis* and *Ctenocystis* have been completely replaced by pyrite (often converted to limonite), or are represented by air-filled holes. No trace of calcite remains. The superficial histological detail is well preserved so that it is possible to recognize the surface features of different types of stereom. On the other hand, all the plates have been distorted tectonically and are often squashed on to the bedding planes.

On the sea-floor, the black shale matrix was probably a stinking black mud. However, there is abundant benthos which indicates that the bottom water was usually oxygenated. Conditions may have resembled those of the German Lower Devonian Hunsrückschiefer, which are similarly black with abundant pyritized benthic fossils. Seilacher and Hemleben (1966) have argued, on the basis mainly of trace fossils, that the Hunsrück-schiefer were normally laid down in oxygenated bottom water, but that sometimes the bottom water lost its oxygen, asphyxiating the benthos. The same may have been true of the sea in which *P. menevensis* lived. As we show later, the species is adapted to staying up on extremely soft mud.

Anatomical description

Introduction. In describing the anatomy of *P. menevensis* we frequently refer, in passing, to related species, since without comparison morphological features have little significance. The particular species compared are: *Ceratocystis perneri* Jaekel from the Middle Cambrian of Bohemia, Czechoslovakia (text-fig. 11); *Nevadaecystis americana* (Ubaghs) from the Upper Cambrian of Nevada (text-fig. 12); *Cothurnocystis elizae* Bather from the Upper Ordovician of Scotland (text-fig. 14); and '*C.*' *fellinensis* Ubaghs, 1969 from the Lower Ordovician of the South of France (text-fig. 13).

To anticipate the arguments given below under 'Systematic Position', *Ceratocystis perneri* is less crownward (less closely related to the chordate crown group) than *P. menevensis*, and in many respects shows the most primitive condition among known cornutes; *N. americana* is more crownward than *P. menevensis*; '*Cothurnocystis*' *fellinensis* is more crownward than *N. americana*; and *C. elizae* is more crownward than '*C.*' *fellinensis* (text-fig. 26). These conclusions are mentioned early so that the anatomical description, which is comparative, will be easier to understand. It is unfortunate that *N. americana* is known only from one specimen and that the floor of the head is not visible from beneath, though partly visible from above.

As regards plate notation, one of us used to employ an objective system (Jefferies 1968) in which marginal plates were numbered from the anterior end of the tail and were given suffixes for left and right, dorsal and ventral (e.g. M_{1LD} was the first left dorsal marginal plate). This system was explicitly intended not to imply homology, so that marginal M_{3L} of *C. elizae*, for example, was not homologous with M_{3L} of *N. americana*—they correspond, respectively, to plates t and l of the comparative notation. In earlier studies of cornutes and mitrates, such an objective system was necessary. However, comparative anatomy depends on recognizing and naming homologies, accepting the risk of thereby making mistakes. Accordingly, a comparative, non-objective plate notation was proposed by Jefferies and Prokop (1972) when describing the crownward cornute
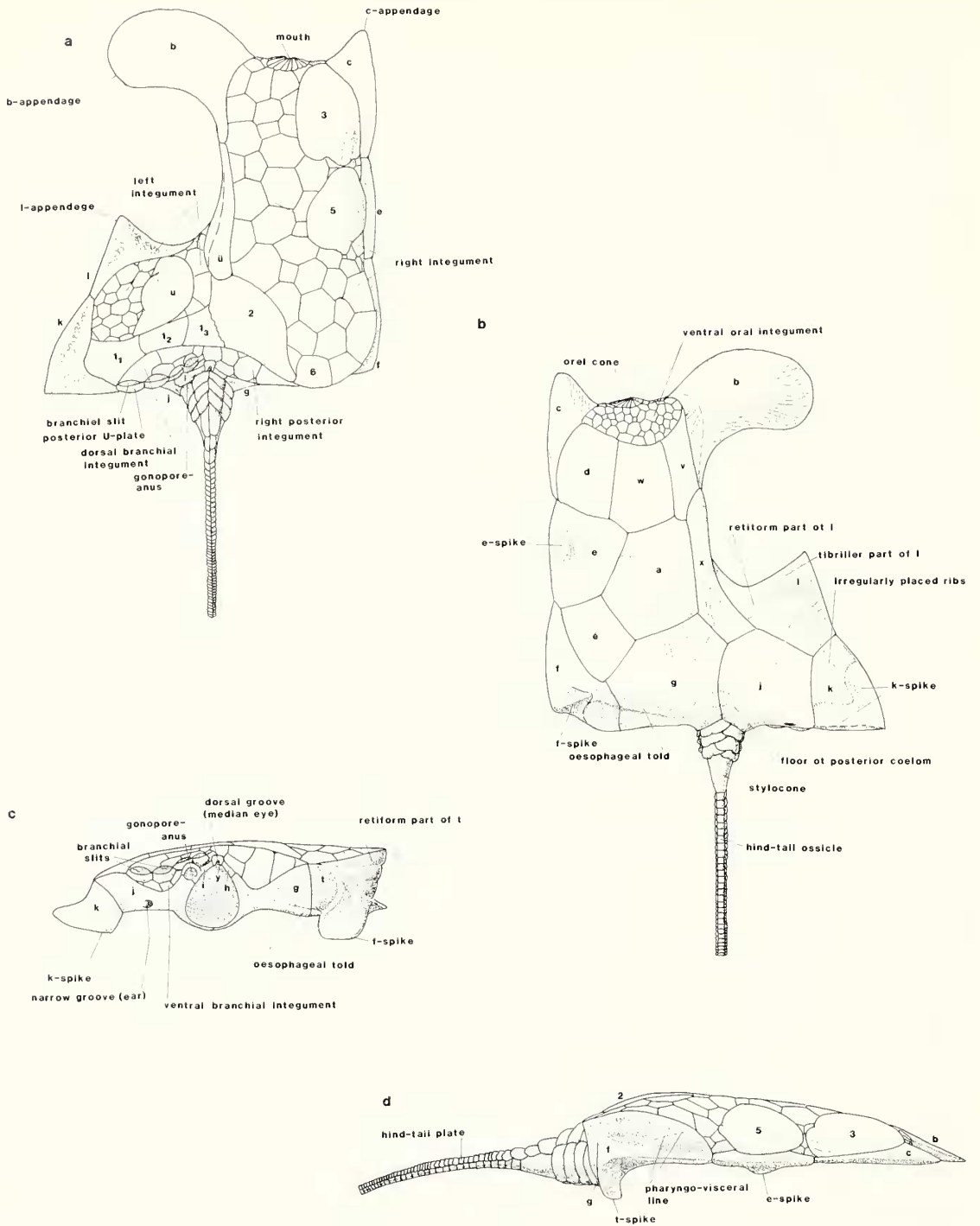
TEXT-FIG. 10. *Protocystites menevensis* Hicks; reconstructed external morphology. *a*, dorsal; *b*, ventral; *c*, posterior; and *d*, right lateral aspects. Letters a–w, é, ü, and numbers 1, 2, 3, 5, 6 indicate plate homologies as explained in text. The exact number of branchial slits is not known.
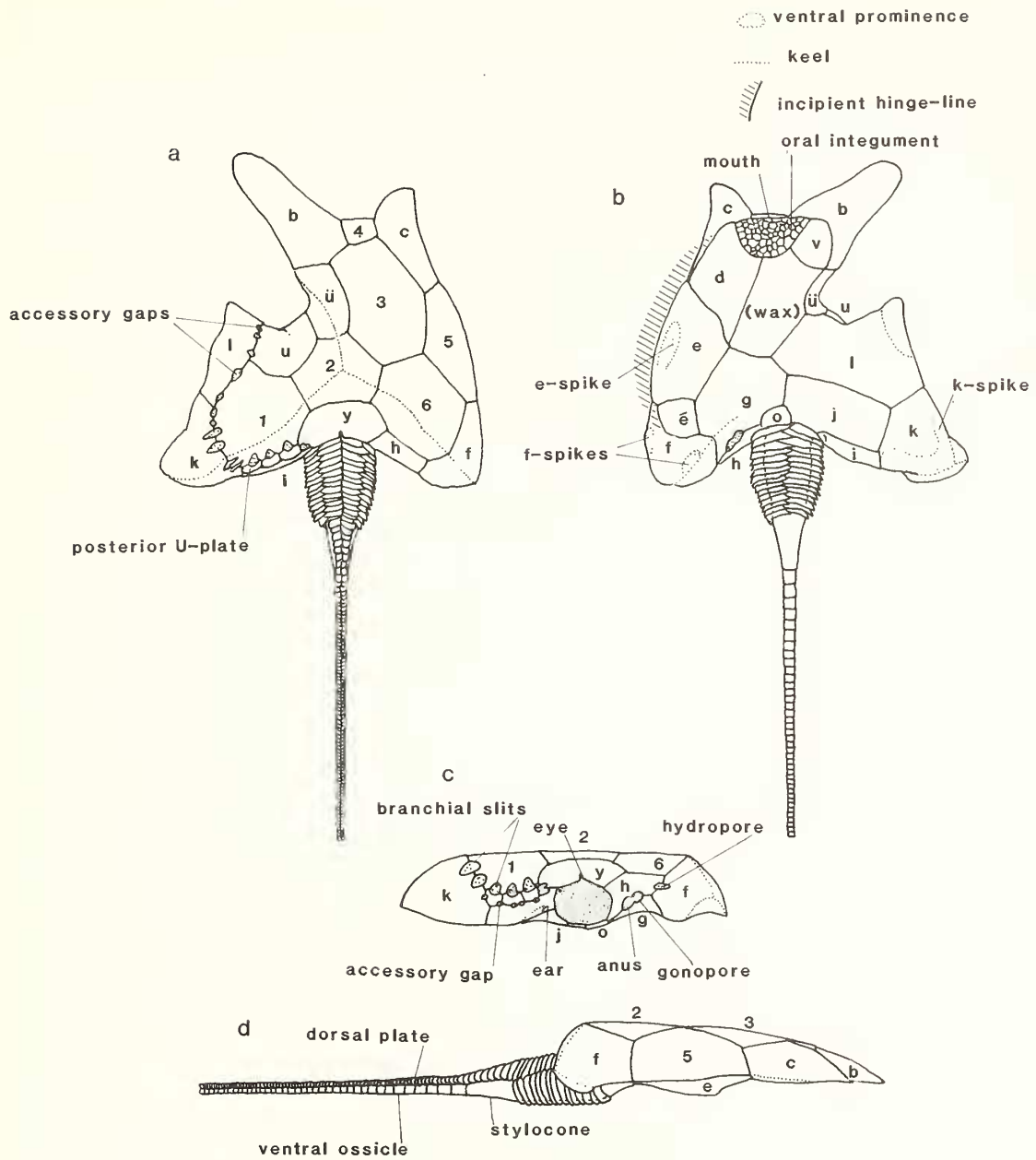
TEXT-FIG. 11. *Ceratocystis perneri* Jaekel; reconstructed external morphology. *a*, dorsal; *b*, ventral; *c*, posterior; and *d*, right lateral aspects.

Reticulocarpos hanusi. In this notation, marginal plates are given lower-case letters of the roman alphabet. The series starts at plate a, which occupies a position near, but not at, the anterior left part of the head, and is followed by plate b just left of the mouth, and so forth in clockwise order in dorsal aspect around the head to finish at plate l in *R. hanusi*. In applying this scheme to species other than *R. hanusi*, additional letters are interpolated as necessary and, since the number of homologous series of marginal plates in cornutes and
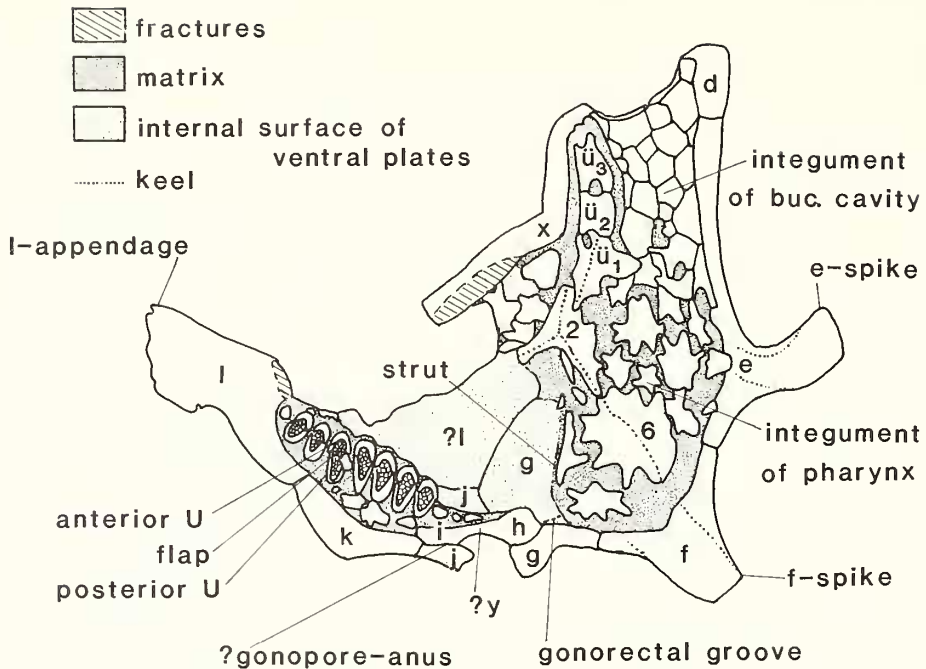
TEXT-FIG. 12. *Nevadaecystis americana* (Ubaghs); Upper Cambrian, Nevada, United States National Museum 143237; diagrammatic drawing of the dorsal aspect of the only known specimen and holotype (redrawn after Jefferies 1969, text-fig. 4).

mitrates now exceeds twenty-six, the English roman alphabet is supplemented by letters from German and French (ü, é, etc). (We do not imply that plate ü has any special relation to plate u, nor plate é to plate e; nor do the U-plates of the branchial slits form part of this notation, for with them the U is upper case and describes the shape of the plates.) For centrodorsal plates, in which homologies can be recognized between *Ceratocystis perneri*, *P. menevensis*, and *N. americana*, the numbers 1 to 6 are employed, starting from the situation in *C. perneri* where the sequence is once again clockwise in dorsal aspect. Suffixes are used when several plates correspond to a single dorsal plate in *C. perneri*. This comparative notation is difficult to memorize, but becomes clear in the text-figures.

Various protuberances were borne on the heads of cornutes and, like the plates, these can now be homologized from species to species. Such processes were of two main types—appendages and ventral spikes—though the distinction between the two is not precise. Appendages made up parts of the anterior margin of the head and projected horizontally, or horizontally and downwards; spikes, by contrast, projected downwards from the ventral surface. Jefferies (1968) used an objective notation for the spikes (S_{1R}, S_{2R}, etc.) much like the notation used for the plates, whereas the appendages were referred to as 'left', 'left oral', and 'right oral'. In this paper, we replace these terms by a new notation which refers to the plate on which the process was carried, e.g. e-spike, l-appendage. As with the plates, the new notation is not objective but implies homology. It is convenient, because a plate in cornutes seldom bears more than one individualized process (though that process is often complicated in shape) and such a process is never constituted from more than one plate.

The nomenclature of different types of stereom follows Smith (1984*b*, fig. 3.2).

General external features and the plates of the head. P. menevensis (text-fig. 10) consisted of a head and a tail, like every other cornute and mitrate. The outline of the head was boot-shaped, as was common among primitive cornutes and it particularly resembled that of *C. perneri* in that plate k extended further leftward than plate l. The right margin of the head, as reconstructed, was almost straight and at right angles to the posterior margin. This could be a mistake in the reconstruction caused by tectonic distortion, but if there is no mistake the right margin of the head was different in shape to that of *C. perneri* in which it ran

leftwards and forwards. In *P. menevensis* it was in this respect probably more like *N. americana*, 'Cothurno-cystis' *fellinensis*, and *C. elizae*.

The ventral surface of the head of *P. menevensis* was made up, except for a small oral integument, of large plates and would have been rigid (Pl. 55, fig. 1). The dorsal surface also contained some large plates, but was mainly covered with plated integument (Pl. 54, fig. 1). This combination of rigid floor and flexible roof is otherwise known in cornutes only in *N. americana*. It was morphologically intermediate between *Ceratocystis perneri*, where the floor and roof were both rigid, and *Cothurnocystis elizae*, for example, where the floor and roof were both flexible though the floor was crossed by a strut. The large plates forming the floor of *P. menevensis* can be called a ventral shield. We shall describe this shield first, before discussing the skeleton attached to it dorsally.
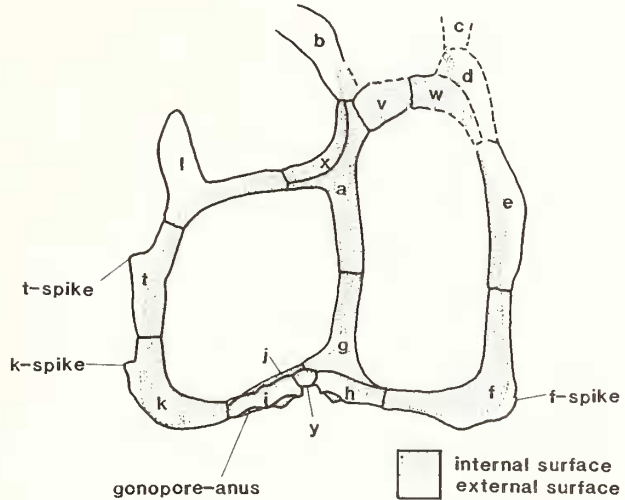

TEXT-FIG. 13. 'Cothurnocystis' *fellinensis* Ub-aghs; Lower Ordovician (probably Lower Ar-enig), Montagne Noire, France; dorsal aspect of marginal skeleton of head (redrawn after Ubaghs 1969, fig. 19).

The right edge of the ventral shield, and of the head, of *P. menevensis* was made up of plates g, f, e, and c. Plate g (Pl. 55, figs. 1 and 3; Pl. 58, fig. 1; Pl. 60, figs. 3, 4, 9, 10) was the first right ventral marginal (M_{1RV} in the old notation) and included the right half of the tail attachment. Much of its posterior part was almost vertical, forming part of the posterior wall of the head. Its anterior part was horizontal, however, forming part of the rigid floor. Where ventral and horizontal portions joined, there was a distinct fold (oesophageal fold), concave dorsally and convex ventrally, which ran rightwards into plate f. Another fold, similarly convex downwards but wider and resembling half of a crescent in plan view, was situated just anterior to the tail attachment and underlay the right half of the posterior coelom (see below, under 'The chambers and soft anatomy of the head').

Plate f (Pl. 54, figs. 1 and 3; Pl. 55, figs. 1, 4, 5; Pl. 56, fig. 1; Pl. 57, figs. 1 and 4; Pl. 58, figs. 1; Pl. 60, figs. 5, 6, 7) formed the posterior right corner of of the ventral shield, i.e. the 'heel' part of the 'boot'. Like plate g, it was divided into a horizontal portion, which was part of the floor, and a vertical portion, which formed part of the posterior and right lateral walls of the head. Plate f was drawn out horizontally into a sharp-edged peripheral flange and the posterior end of this flange was turned downwards to form the f-spike. Plate f carried the right end of the oesophageal fold, the rest of which was on plate g.

Plate e (pl. 54, figs. 1–3; Pl. 55, fig. 1; Pl. 56, fig. 1; Pl. 57, fig. 3; Pl. 58, fig. 4) formed the middle part of the right edge of the ventral shield. It had a sharp-edged peripheral flange which was continuous with that of plate f and which ran forward into that of plate c. In dorsal aspect it showed, on the right, a distinct marginal frame, the middle part of which articulated with dorsocentral plate 5. On the ventral surface of plate e there was an e-spike, homologous with that of other cornutes. We use the term 'spike' for consistency with other cornutes, though the word is not totally appropriate in *P. menevensis* since the process was rounded in shape and, in particular, had the same slope in all directions, whereas most spikes in cornutes have the anterior slope steeper and sharper than the posterior one. The e-spike of *P. menevensis* was hollow, corresponding to a circular concavity in the internal dorsal face of plate e.
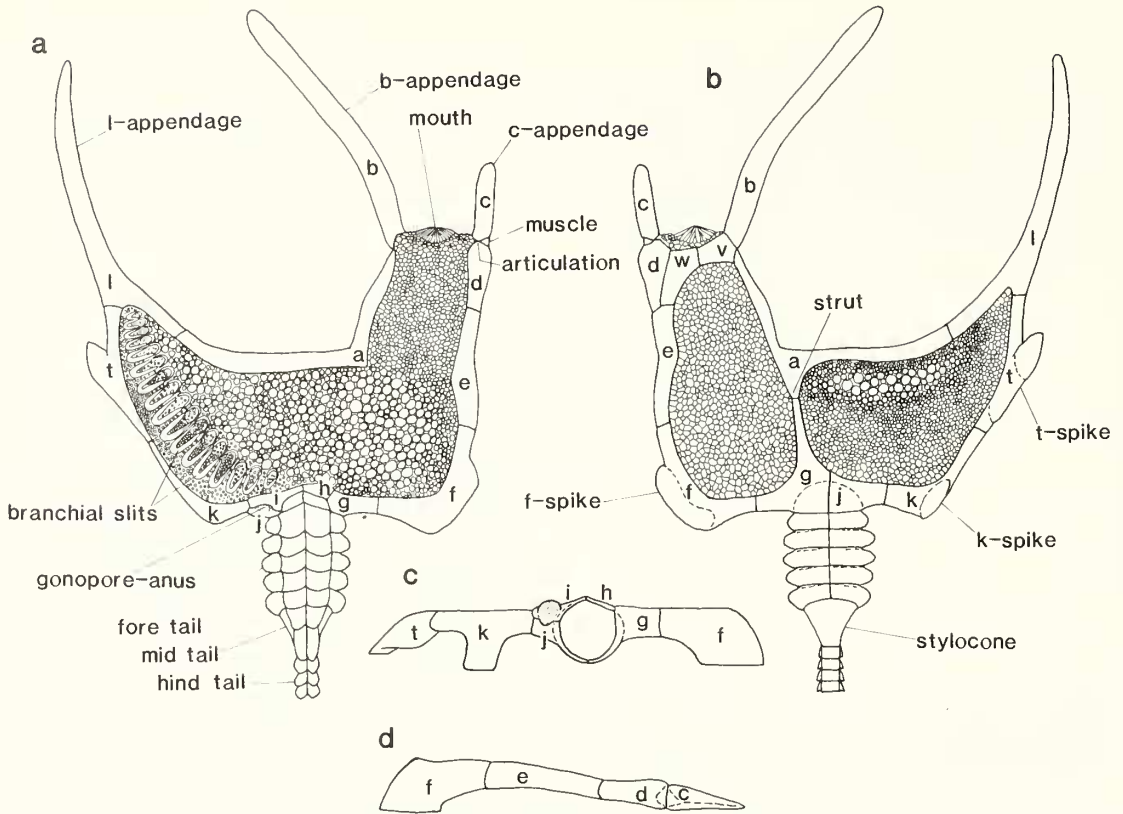
TEXT-FIG. 14. *Cothurnocystis elizae* Bather; Upper Ordovician (Ashgill), Girvan, Scotland (redrawn after Jefferies 1968, text-fig. 1), with most of the hind tail omitted. *a*, dorsal; *b*, ventral; *c*, posterior; and *d*, right lateral aspect of right side of frame only.

Plate c (Pl. 54, figs. 1 and 3; Pl. 55, fig. 1; Pl. 58, fig. 1), which included the c-appendage (right oral appendage), was the most anterior plate on the right side of the ventral shield. It had a sharp-edged keel which was a forward continuation of the peripheral flange of plate e. It was ventrally convex and dorsally plane. Dorsally it articulated with, or was lightly sutured to, dorsocentral plate 3.

The left edge of the ventral shield was formed of plates j, k, l, x, and b. Plate j, which is not well shown in any specimen (but see Pl. 54, fig. 4; Pl. 55, fig. 1; Pl. 56, fig. 3; Pl. 57, fig. 1) was the first left marginal (M_{1LV} of the old notation). It had a vertical portion, forming part of the posterior wall of the head, and a horizontal portion included in the floor. Plate j carried the left half of the tail insertion. A ventrally convex portion of it, resembling half a crescent in plan view, lay just anterior to the tail and was the floor of the left half of the posterior coelom. In the leftward portion of the plate the junction between the horizontal and the vertical parts was abrupt and presented an almost rectangular keel on the external surface. Just dorsal to this keel was an opening (Pl. 55, figs. 1 and 2) which corresponded in general position to the narrow groove of *Ceratocystis perneri*, though it penetrates plate j and not plate i as in *C. perneri*. The opening probably represented an ear, functioning as lateral line, and was thus a primitive representation of the acustico-lateralis system (Jefferies 1969, p. 522; 1986, Ch. 7). Dorsally and towards the median line, plate j of *P. menevensis* would have articulated with plate i and was notched by the ventral margin of the gonopore-anus.

Plate k (Pl. 54, figs. 1, 2, 4; Pl. 55, fig. 1; Pl. 56, fig. 1; Pl. 57, fig. 1; Pl. 58, fig. 1; Pl. 60, fig. 1) of the ventral shield of *P. menevensis* was triangular in plan view and was the leftmost plate in the head. Its horizontal portion made part of the floor and was sharply distinct from the vertical portion which formed part of the posterior and left lateral walls of the head. There was a ventral k-spike (Pl. 60, fig. 1) which was V-shaped,

with the limbs of the V running respectively along the left boundary and posterior boundary of plate k. The smooth, outward-facing surfaces of the spike were continuous, respectively, with the posterior and left lateral walls of the plate and were almost vertical. The inward-facing surfaces of the spike were rough and made an angle of *c.* 45° to the horizontal. (The corresponding k-spike of *C. perneri* (text-fig. 11) was similarly V-shaped, though much less well marked than that of *P. menevensis*.) In dorsal aspect, plate k of *P. menevensis* showed a keel which ran forward and rightward from the left corner of the head up towards the dorsal surface. The dorsal edge of plate k (Pl. 60, fig. 2), unlike that of *C. perneri*, was entire and not notched for branchial slits.

Plate l (Pl. 55, fig. 1; Pl. 57, fig. 1; Pl. 58, figs. 1 and 3) lay anterior to plate k and consisted of two portions abruptly separated from each other—the marginal frame and the horizontal lamina. The frame made part of the left wall of the head while the lamina formed part of the floor. The frame extended into a sort of wing— the l-appendage (left appendage)—which was approximately horizontal in disposition, or possibly sloped downwards and forwards to judge by the situation in *C. perneri*. The edge of the l-appendage was continuous posteriorly with the keel that separated the horizontal portion from the left vertical portion of plate k. Anteriorly the edge of the l-appendage passed into a keel which became less and less distinct, to disappear approximately at the anterior border of the plate.

Plate x (Pl. 55, fig. 1; Pl. 58, fig. 1) was elongate and only its anterior third contributed to the left margin of the head and ventral shield and to the left lateral wall. Posteriorly it was horizontal and ran rearward to abut against plates g and j.

Plate b (Pl. 54, fig. 1; Pl. 55, fig. 1; Pl. 58, fig. 1; Pl 59, figs. 2–4) included the b-appendage (left oral appendage) and was the most anterior plate of the left side. Like plate c on the other side of the mouth, it was convex ventrally and flat dorsally. Unlike plate c, however, there was a thin laminar portion of plate b which extended rightwards to form part of the floor.

Other plates made part of the ventral shield but did not contribute to its right and left edges in ventral aspect. These were plates d, w, and v (Pl. 55, fig. 1; Pl. 58, fig. 1) behind the oral integument, and plates a and é whose positions were more central. Plates d, w, and v made a post-oral series and their anterior outlines were concave where they abutted against the oral integument. The position of plate d thus resembled that of the same plate in *C. perneri* (text-fig. 11*b*), while in *Nevadaecystis* and all cornutes more crownward than it, plate d had become a marginal plate inserted between plates e and c (text-figs. 12–14). Plate a was a large polygonal plate of central position in *P. menevensis*, whereas plate é was a smaller plate situated between plates a and f. (*C. perneri* likewise had a plate é, but also a single large plate corresponding to plates w + a + x of *P. menevensis*.) In '*Cothurnocystis*' *fellinensis* (text-fig. 13) and many more crownward cornutes, on the other hand, plate a was a marginal plate forming the anterior part of the strut and the adjacent parts of the frame. In many crownward cornutes, including *C. elizae* (text-fig. 14), plate x did not exist, whereas in *C. fellinensis* it was a marginal plate overlying parts of plate a.

Concerning the strut, which crosses the head from front to rear in most cornutes, the situation in *P. menevensis* is complicated. The strut of *C. elizae* (text-fig. 14), for instance, was formed of parts of plates g and a and it divided the ventral integument into two parts. Such was the usual situation in cornutes, as seen also in '*C.*' *fellinensis* (text-fig. 13), for example. In *Nevadaecystis*, which so far as can be seen had a rigid floor, the strut was represented by a thickening of plate g which ran forward and presumably continued on to plate a (though that plate is not visible on the only known specimen). There was no trace of such a single thickening on plates g or a of *P. menevensis*. Ribs existed and ran more or less radially out from the growth centres on the thinner parts of plates g, a, j, k, l, x, and b (the laminar part of this plate). However, the ribs were irregular in position and numerous, and none of them can certainly be identified with portions of the strut of other cornutes. Perhaps they represented a primitive, unfixated condition, two apposed ribs of which alone survived to give the strut of more crownward cornutes.

An alternative possible evolutionary beginning for the strut is represented in *P. menevensis* by an internal process on plate g (cleft on the internal mould, text-fig. 23*a*; Pl. 55, fig. 3; Pl. 60, figs. 3, 9, 10) situated between the posterior coelom and the right anterior coelom (see below, under 'The chambers and soft anatomy of the head'). If it grew forward during evolution, this process would produce a thickening in the same position as the strut of *N. americana*. In broad terms, however, it is true to say that *P. menevensis* had no strut, or at least, no strut that can certainly be homologized with the strut of cornutes more crownward than *P. menevensis*. The absence of such a strut is probably primitive and likely to be homologous with its absence in *Ceratocystis perneri*. Mechanically speaking, the strut of cornutes would have served mainly to prevent the head being crushed under anteroposterior compression. This function would have been carried out in *P. menevensis* by the triple arch of the dorsal surface (see below), in collaboration with the rigid floor of the head. This also is probably primitive, since the head of *P. menevensis* to this extent retained the box-like construction of the head of *C. perneri*.

TEXT-FIG. 15. Half-scale, outline drawing of Plate 54, fig. 1. For single letters or numbers, see plate notation shown in text-fig. 10. Other labels: 1/2, surface on plate 2 representing articulating junction with plate series 1; cb, cerebral basin; dbi, dorsal branchial integument; ga, gonopore-anus; li, left anterior integument; pu, posterior U-plate; oc, oral cone; stc, stylocone; ri, right integument; vo, ventral ossicle of hind tail.
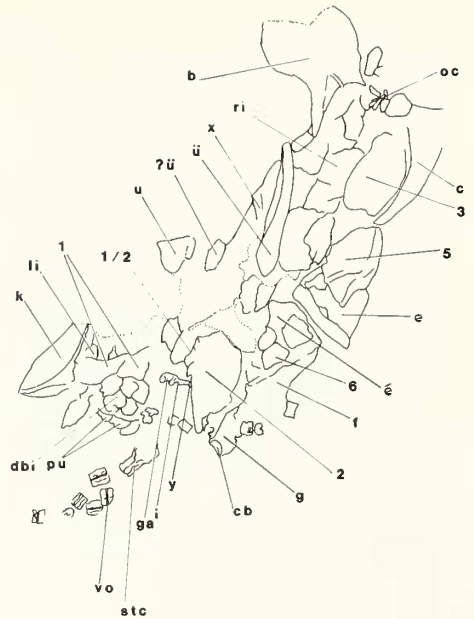
As to the stereom of the ventral shield, the central part, which was stiffened by ribs, consisted of extremely thin, retiform stereom, except for the ribs themselves which were of labyrinthic stereom and were more convex externally than internally. This type of structure, consisting of a web with struts, would be described by architects as a space frame. It would have combined lightness with stiffness and suggests that *P. menevensis* was adapted for low weight. More peripherally, the ventral shield tended to be thicker. Sometimes it was of perforate stereom externally, but smooth and almost imperforate internally, as in the posterior right-hand part of the floor (plate é and the adjacent parts of plates e, a, and g) where it underlay the cavity of the right anterior coelom (see below, under 'The chambers and soft anatomy of the head'), and also in plates g and j beneath the posterior coelom. The peripheral parts of the ventral shield tended to be formed of labyrinthic stereom, though the sharp edges were sometimes of fibrillar stereom. Thus the oral appendages of plates b and c were covered on their convex ventral surfaces with a sheet of fibrillar stereom (Pl. 55, fig. 1; Pl. 59, figs. 3 and 4), the fibrils being more or less radial in arrangement. But the flat dorsal surfaces of these plates (Pl. 54, fig. 1; Pl. 59, fig. 2) were formed of labyrinthic stereom, except peripherally; this labyrinthic stereom filled, so to speak, the dorsal concavity of the ventral fibrillar layer. Again, in plate l, the posterior parts of the plate, forming part of the floor, were of space-frame type (Pl. 55, fig. 1; Pl. 57, fig. 1; Pl. 58, fig. 3; Pl. 60,

EXPLANATION OF PLATE 54

Figs. 1–4. *Protocystites menevensis* Hicks. 1–3, BM(NH) E62963 from loc. 2, Porth-y-rhaw (see text-fig. 7); *Hypagnostus parvifrons* Zone, Middle Cambrian. This is the best specimen known. Plate e has been dislocated and rotated approximately 90° from its original position. 1, general dorsal aspect of latex cast (see text-fig. 15 on facing page), × 6·9. 2, latex of posterior left part of head at an earlier stage of dissection than in fig. 1; note the series of plates 1, × 11·9. 3, plate 3 at a higher magnification than in fig. 1 and oriented as in the reconstruction in text-fig. 10, × 12·8; is, imperforate stereom of plate e; rs, retiform stereom of plate e; pbbc, callus marking posterior boundary of buccal cavity. 4, BM(NH) E62979, also from loc. 2, Porth-y-rhaw. Latex in dorsal aspect; note posterior coelom (pc) clearly defined by an arcuate ridge on the dorsal surface of plates g and j; note also the vertical wall (vw) which represented the posterior limit of the posterior coelom and which formed the front wall of the cerebral basin, × 4·2.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.
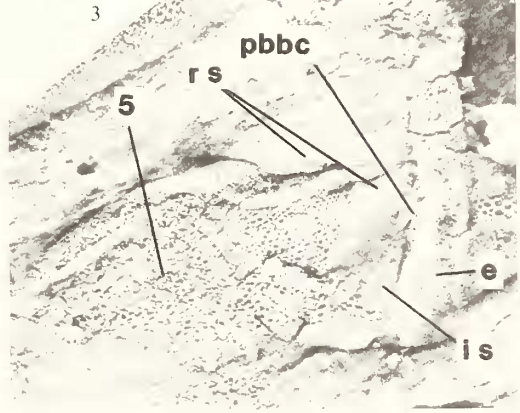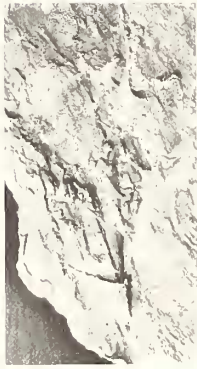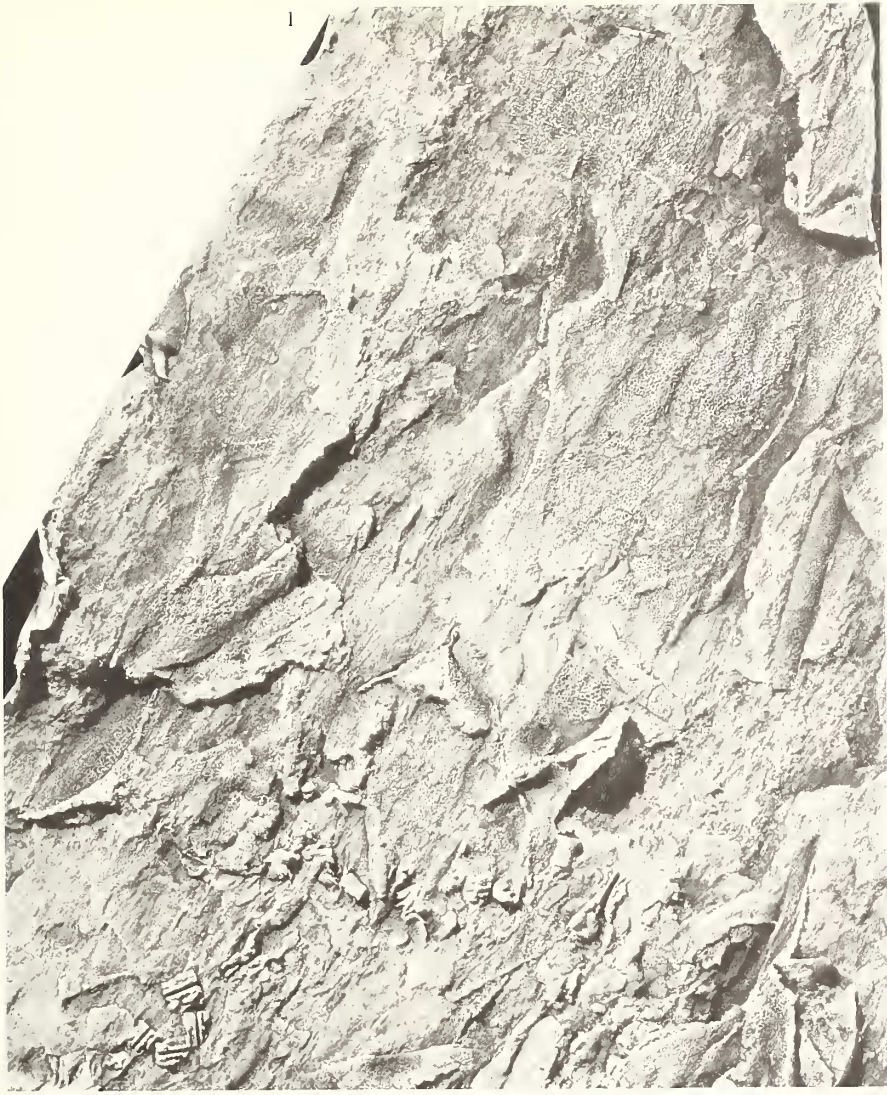
PLATE 54

JEFFERIES, LEWIS and DONOVAN, *Protocystites*

TEXT-FIG. 16. Half-scale, outline drawing of Plate 55, fig. 1. For single letters or numbers, see plate notation shown in text-fig. 10. Other labels: esp, e-spike; fsp, f-spike; ft, fore tail; kj, keel on plate j; lf, fibrillar part of l; lr, retiform part of l; ng, narrow groove (ear) in plate j; oc, oral cone; oi, oral integument; stc, stylocone; vo, ventral ossicle of hind tail.
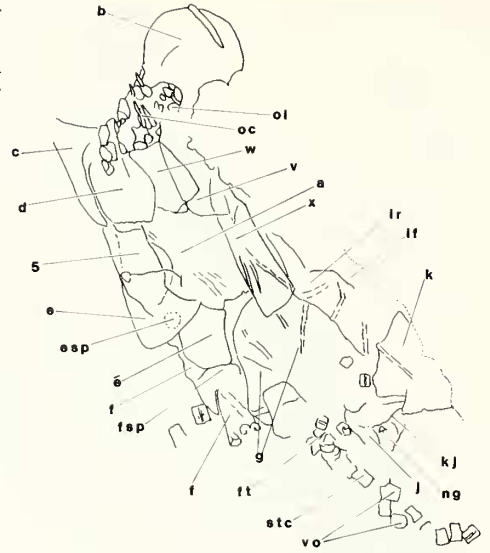

fig. 8), but the vertical wall was of labyrinthic stereom and the l-appendage was fibrillar stereom, with the fibrillae running parallel to the anterior edge of the appendage. The stereom of plate f was particularly complicated. The spike and peripheral flange seem to have been built of labyrinthic stereom which was particularly dense at the sharp edges. Most of the lateral wall of plate f, however, was of very thin retiform stereom crossed by horizontal folds (pw in Pl. 57, fig. 4; Pl. 60, figs. 5–7). This thin part of the wall corresponds to the presence of a pharynx inside the head, as argued below.

The dorsal surface of the head, as already mentioned, contained some regular, individualized plates separated by plated integuments. The first group of individualized plates to be described is the dorsal arch of the tail insertion, consisting of plates h, y, and i (M_{1RD}, M_{PD}, and M_{1LD} of the old notation). Of these, plate y (Pl. 58, fig. 2) formed the keystone of the arch, being median and dorsal in position; its posterior, external surface was notched from below by a groove (the dorsal groove) which in life probably carried a median eye that arose from the dorsal surface of the brain. Plate i (Pl. 54, fig. 1), forming the left part of the arch, ran between plates y and j; at its ventral end it had a large, almost circular embayment which in life carried the gonopore-anus. Plate h (Pl. 54, fig. 4) ran between plates g and y and formed the right part of the dorsal arch.

A comparison of the plates and openings near the tail attachment with those of other cornutes is of interest. Compared with *C. perneri* (text-fig. 11), in *P. menevensis*: 1, the gonopore-anus was left of the tail, not right of it; 2, there was no plate o (M_{PV} of the old notation); 3, plate g formed part of the tail attachment, had a much larger ventral posterior portion, and did not abut against the gonopore-anus; 4, plate j formed a larger part of the tail attachment, had a larger vertical wall, included the narrow groove (ear) (which in *C. perneri* was in i), and formed the lower boundary of the gonopore-anus; 5, plate i was much smaller, contained the


EXPLANATION OF PLATE 55

Figs. 1–5. *Protocystites menevensis* Hicks. All specimens from loc. 2, Porth-y-rhaw. 1, BM(NH) E62963, latex of ventral aspect of best specimen (see text-fig. 16 on facing page), × 6·9. 2, detail of same to show plate j with ear (ng, narrow groove), × 8·8. 3, BM(NH) E62958, natural moulds of internal surfaces of two specimens of plate g, in ventral aspect, suggesting the soft parts (cf. text-fig. 22a), × 8·4; br, brain; cl, cleft between posterior coelom and right anterior coelom; gr, gonoduct-rectum; ocs, oesophagus; pc, posterior coelom; st, change in nature of stereom from almost imperforate at right posterior to thin and retiform at left anterior (retiform stereom has a granular appearance). 4, 5, BM(NH) E63034, latexes of plate f in ventral and dorsal aspect; oesf, oesophageal fold; fsp, f-spike; 4, × 10·3; 5, × 11·8.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.
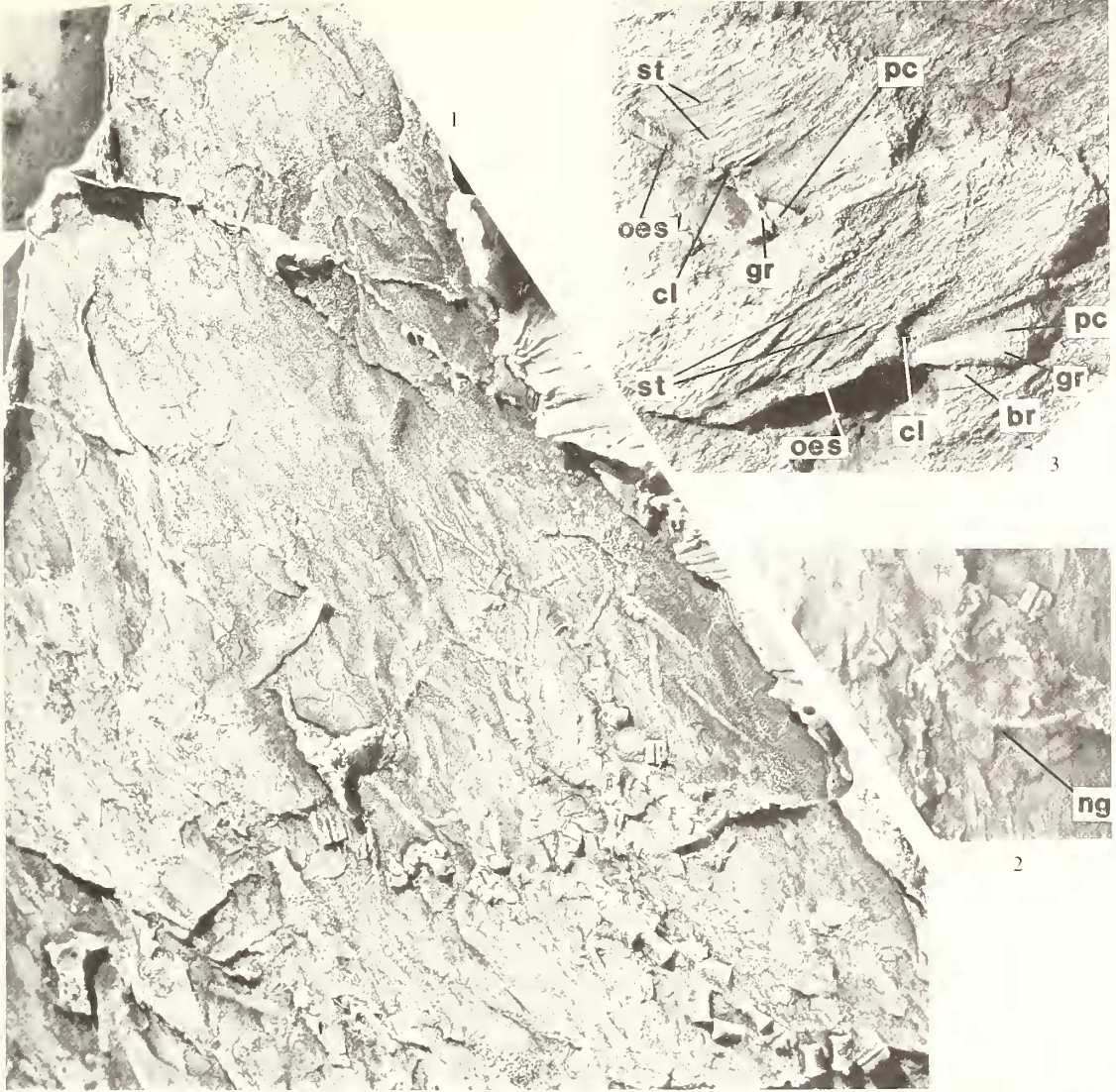
PLATE 55

TEXT-FIG. 17. Half-scale, outline drawing of Plate 56, fig. 1. For single letters or numbers, see plate notation shown in text-fig. 10. Other labels; ai, almost imperforate stereom in plate a; D, dorsal plate of fore tail; ar, reticulate stereom in plate a; dp, dorsal plate of hind tail; ef, frame part of plate e; ei, almost imperforate stereom in plate e; fsp, f-spike; h esp, hollow in interior of plate e, corresponding to e-spike; li, left anterior integument; pbbc, callus marking posterior boundary of buccal cavity; ri, right integument; stc, stylocone; vo, ventral ossicle of hind tail.
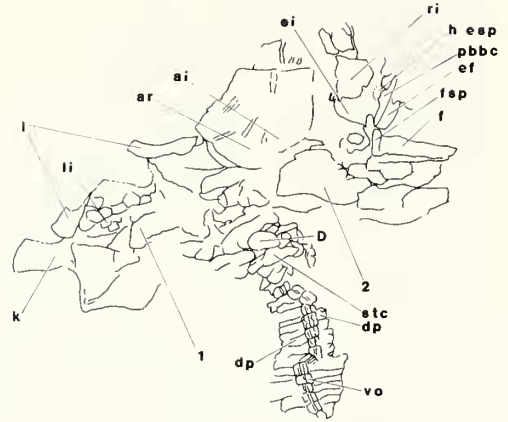
dorsal boundary of the gonopore-anus, and was dorsolateral in position with respect to the tail attachment, instead of lateral—indeed, much of plate i as seen in *C. perneri* seems to be replaced by integument in *P. menevensis*; 6, plate y was much smaller and bounded anteriorly by integument; 7, plate h was likewise much smaller and bounded anteriorly by integument, was perhaps partly replaced by integument, and did not abut against the gonopore-anus nor the hydropore (which in *P. menevensis* was absent, see below). These differences are in some cases interrelated: thus, the fact that plate g in *P. menevensis* made no contact with the gonopore-anus is due to the position of the latter left of the tail. With one exception, however, all these differences from *C. perneri* are resemblances to '*Cothurnocystis*' *fellinensis* (text-fig. 13) and probably to *N. americana* also (text-fig. 12), whose morphology is less well known. The exception relates to the ear, whose position penetrating plate j (text-fig. 11*b*, *c*; Pl. 55, fig. 2) could be a specialization of *P. menevensis*, though the fact that it was not conflated with the gonopore-anus was a resemblance to *Ceratocystis perneri*. These differences from *C. perneri* are also resemblances to *Cothurnocystis elizae* (text-fig. 14)—the best studied *Cothurnocystis*—except that *C. elizae* lacked plate y, the median eye, and plate x.

A three-legged arch occupied the central part of the dorsal surface of the head. The largest plate in this arch was dorsocentral 2 (Pl. 54, figs. 1 and 4) which lay to the right of the mid-line of the tail and probably


EXPLANATION OF PLATE 56

Figs. 1–5. *Protocystites menevensis* Hicks. 1–3, SM A.1021, lectotype (see also Pl. 57, figs. 1 and 2), *ex* Hicks's Collection; Menevian, Porth-y-rhaw, Dyfed. [The specimen was cleaned in thioglycollic acid which had the unintended effect of removing all pyrite. The gonorectal groove, which was filled with pyrite and showed clearly when the specimen was first seen, is no longer preserved in the cleaned specimen.] 1, latex of dorsal surface of cleaned specimen (general view), showing that it is dislocated; in particular, plate e is pushed against plate f, and plate f has been inverted so that it here shows the ventral aspect with its f-spike (see text-fig. 17 on facing page), × 5·8. 2, portion of hind tail, at higher magnification, to show features of the dorsal plates; the left dorsal plates have rotated outwards and show their internal surfaces, whereas the right plates show their external surfaces (cf. text-fig. 25), × 18·9; ap, articular process; crf, crescentic facet; fp, fibrillar part of dorsal plate; if, inter-plate facet; ms, median suture (i.e. edge of the dorsal plate where it met the median suture); pol, posterior lobe of dorsal plate; tg, transverse groove. 3, plaster cast of a latex made before the specimen was cleaned with thioglycollic acid and which represents the original shape of the natural mould; ventral aspect of region of the posterior coelom (pc) and of the infilling of the gonorectal groove (gr), i.e. mould of the dorsal surfaces of plates g and j; note that the infilling of the gonorectal groove crosses the posterior coelom and ends at the gonopore-anus (ga) to the left of the tail, towards the bottom right of the figure, × 7·5; g/j, suture between plates g and j. 4 and 5, BM(NH) E62920, latexes of left and right aspects of a specimen consisting of ossicles of the mid and hind tail, still articulated with each other but separated from all other plates, both × 7·0.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.

PLATE 56

JEFFERIES, LEWIS and DONOVAN, *Protocystites*
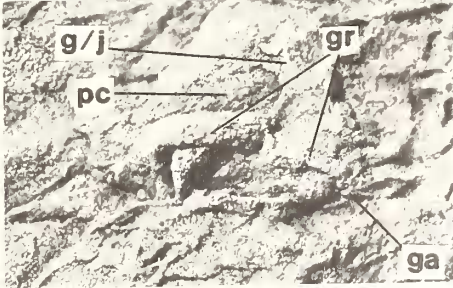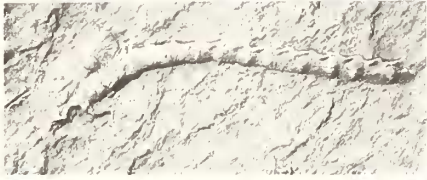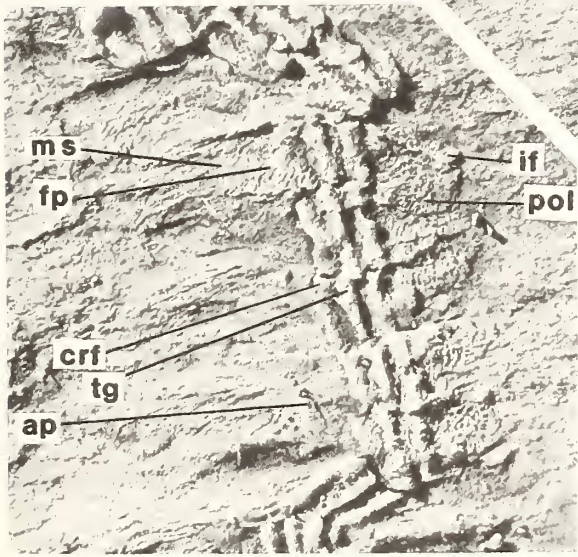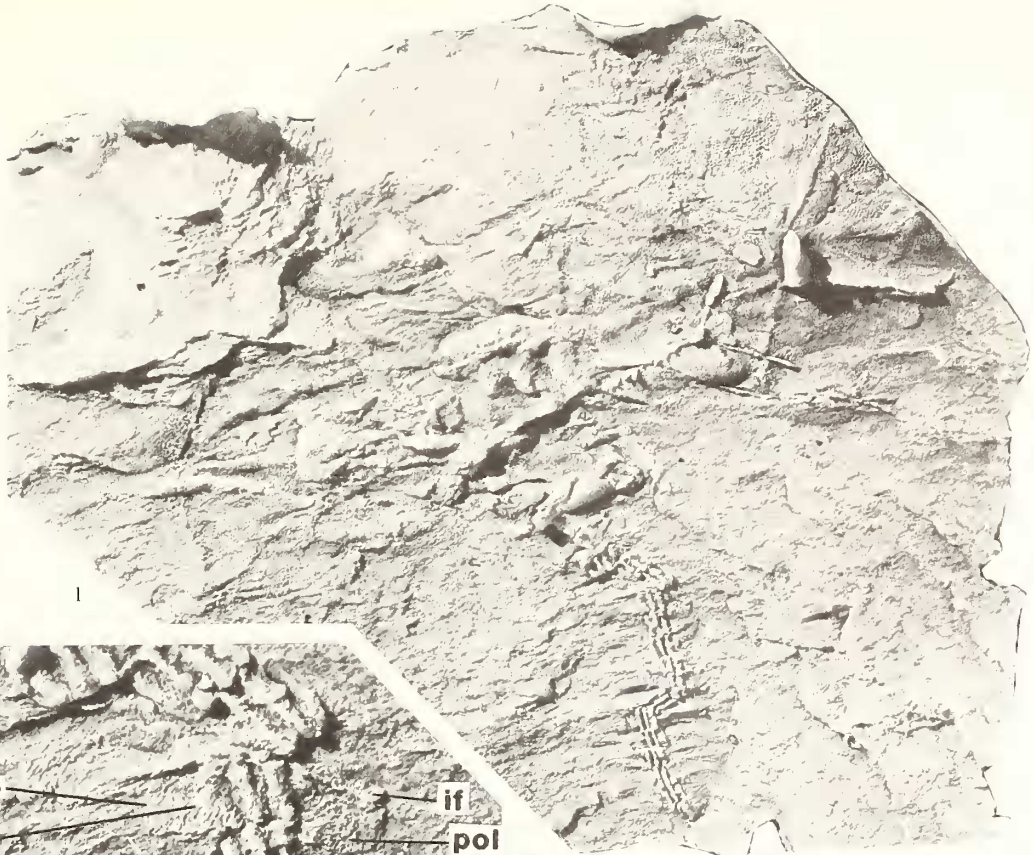
TEXT-FIG. 18. Half-scale, outline drawing of Plate 57, fig. 1.
For single letters or numbers, see plate notation shown in
text-fig. 10. Other labels: dp, dorsal plate of hind tail; lf,
fibrillar part of l; li, left anterior integument (ventral surface
exposed); lr, retiform part of l; oesf, oesophageal fold; stc,
stylocone; vo, ventral ossicle of hind tail; V, ventral plate of
fore tail.
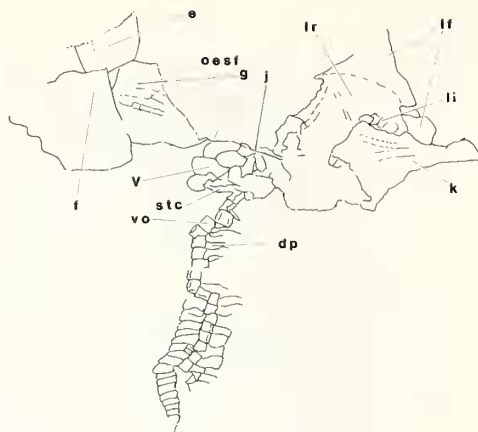
contained the summit of the triple arch. A blunt curved ridge on plate 2 followed its left posterior edge. The
posterior articulation of plate 2 is uncertain; it may have made direct contact with the marginal frame near
the suture of plates f and g; on the other hand, it may have linked with dorsocentral plate 6, which itself made
contact with the frame at plate f. The uncertainty is caused by the fact that the plate identified as dorsocentral
6 may in fact have been only an integument plate thickened along its posterior margin (Pl. 54, fig. 1). Plate 2
made contact on its left with a series of plates (1_1, 1_2, 1_3, etc.; Pl. 54, figs. 1, 2, 4; Pl. 56, fig. 1) perhaps variable
in number, which passed leftwards to meet the vertical keel on the dorsal surface of plate k. The plates of this
series were convex upwards and formed the crest of a gentle ridge which stretched between plates 2 and k.
The third leg of the triple arch was plate ü (Pl. 54, fig. 1): this had a distinct keel, being inverted L-shaped in
section. It contacted plate b anteriorly and plate x ventrally, and it probably articulated directly with plate 2.
On the other hand, an additional plate ($ü_2$; ?ü in text-fig. 15) may have been interpolated between plates ü
and 2 in life (although, if so, it has been considerably displaced after death in the one specimen where it was
seen). The same triple arch can be recognized in *Ceratocystis perneri*, where it was made up of plates 1, 2, ü,
and 6, and formed most of the rather solid roof of the head. It also existed in *N. americana*, though plate ü
was divided there into at least three plates and the equivalents of plate 1, which may have existed in life, are
not preserved in the only known specimen.

Three other individualized plates existed on the dorsal surface: plates u, 3, and 5. Plate u (Pl. 54, fig. 1) lay
anterior to plates 1_1, 1_2, and 1_3 and has only been seen on one specimen. It carried an elongated ridge, as also
did plate u of *C. perneri*, but the orientation and outline of the plate are uncertain. Plates 3 and 5, likewise
only known in the specimen shown in Pl. 54, fig. 1, have already been mentioned as making contact respectively
with plates c and e of the ventral shield.

Plated integument formed the rest of the dorsal surface. The largest such stretch of integument lay to the
right of the triple arch, ran forward to the mouth and over the front margin of the head into the oral
integument of the ventral surface, and was limited on the right and posteriorly by the plates of the ventral

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EXPLANATION OF PLATE 57

Figs 1-4. *Protocystites menevensis* Hicks. 1 and 2, SM A.1021, latex of the lectotype, *ex* Hicks's Collection;
    Menevian, Porth-y-rhaw, Dyfed (see also Pl. 56, figs. 1-3). 1, general view of ventral aspect (see text-fig. 18
    on facing page), × 5·8. 2, portion of hind tail, × 18·9; fp, fibrillar portion of dorsal plate; vp, thick ventral
    portion of dorsal plate; if, inter-plate facet. 3, BM(NH) E62958, from loc. 2, Porth-y-rhaw (see text-fig. 7);
    latex of plate e in ventral aspect with boss-like e-spike (same plate as in Pl. 58, fig. 4), × 5·0. 4, BM(NH)
    E62965, also from loc. 2, Porth-y-rhaw; natural mould of inside of plate f in right posterior aspect (cf. Pl.
    60, fig. 8), × 6·3; fsp, f-spike; int, intestine; pw, pharyngeal wall; pvl, pharyngo-visceral line; sto, stomach.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all
    figs. whitened with ammonium chloride sublimate.
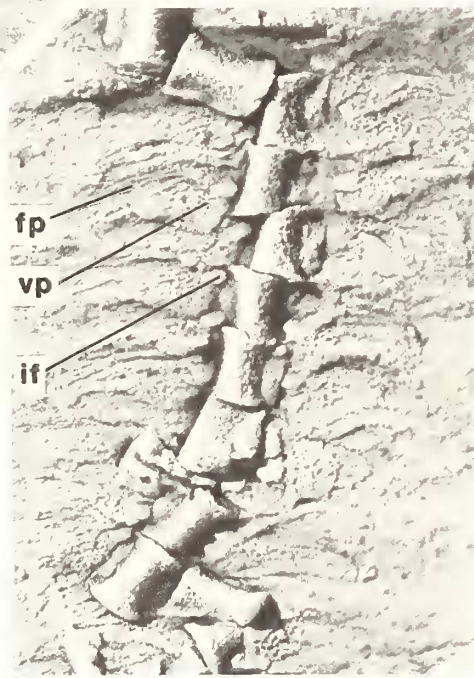
PLATE 57

TEXT-FIG. 19. Half-scale, outline drawing of Plate 58, fig. 1. For single letters, see plate notation in text-fig. 10. Other labels: dp, dorsal plate of hind tail; fsp, f-spike; ft, fore tail; oi, oral integument; stc, stylocone; vo, ventral ossicle of hind tail.
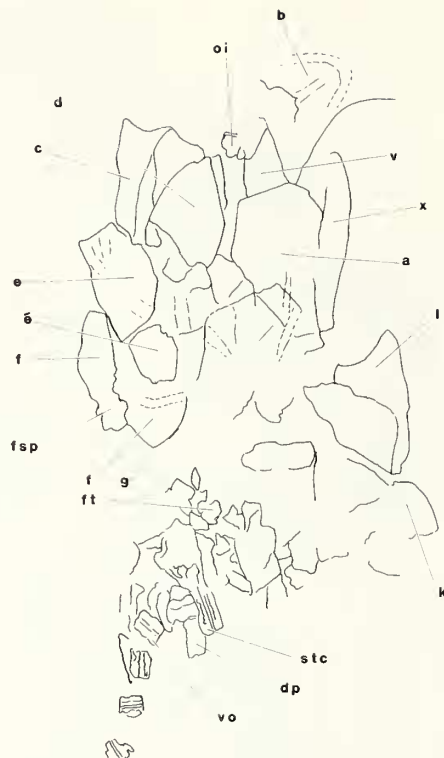
shield (Pl. 54, fig. 1); we refer to it, including the oral integument behind the mouth on the ventral surface, as the right integument. The second largest patch of integument lay to the left of, and anterior to, the triple arch and surrounded, or almost surrounded, plate u (Pl. 54, figs. 1 and 2; Pl. 56, fig. 1); we call it the left anterior integument. The third largest patch of integument lay behind the triple arch, between it and the posterior wall of the ventral shield and dorsal arch of the tail attachment; we call it the posterior integument. To the left of the tail, the posterior integument was presumably penetrated by branchial slits and consisted of rather thick plates, some of which were half-moon shaped and probably homologous with posterior U-plates (pu in text-fig. 15). Well differentiated anterior and posterior U-plates surrounding *elizae*-type slits ('cothurnopores') did not exist in *P. menevensis*, unlike *N. americana*.

As to their stereom, the plates of the right integument were very thin near the posterior part of the head and made up of a single layer of retiform stereom (Pl. 54, fig. 1). Other integument plates were thicker and made up of at least two layers of retiform stereom. The stereom of the dorsocentral plates, and also plates u and ü, was thicker again and tended to be labyrinthic.

EXPLANATION OF PLATE 58

Figs. 1–4. *Protocystites menevensis* Hicks. 1, BM(NH) E432, *ex* Hicks's Collection; Menevian, from near St. David's; latex of ventral surface (see text-fig. 19 on facing page), × 12·8. 2, BM(NH) E63011, from loc. 2, Porth-y-rhaw (see text-fig. 7); latex of plate y in external aspect to show dorsal groove (dg) for median eye, × 19·2. 3, BM(NH) E63008, from loc. 2, Porth-y-rhaw; latex of plate l in dorsal aspect (same plate as in Pl. 60, fig. 7), × 4·6. 4, BM(NH) E62958, from loc. 2, Porth-y-rhaw; latex of plate e, dorsal surface (same plate as in Pl. 57, fig. 3), × 8·3; is, imperforate stereom; pbbc, posterior boundary of buccal cavity; rs, retiform stereom.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.
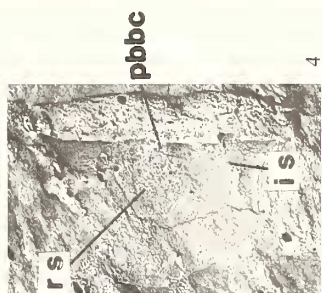
PLATE 58

JEFFERIES, LEWIS and DONOVAN, *Protocystites*

The openings of the head. All of these have already been mentioned in describing the external features of the head skeleton. They are crucial in understanding the anatomy, but we shall identify them without giving reasons—the arguments for these identifications are to be found in Jefferies (1986, Chs. 7 and 8).

The mouth was near the anterior end of the head, between the oral-appendage plates (b and c) and anterior to the approximately semicircular oral integument of the ventral surface. It seems to have been guarded by an oral cone (oc of text-fig. 15, cf. Pl. 54, fig. 1; text-fig. 16, cf. Pl. 55, fig. 1) of radially disposed elongated plates. This mouth would therefore be like that of *Cothurnocystis elizae* in position and in having an oral cone. It differed from the mouth of *Ceratocystis perneri* in having an oral cone and in having flexible integument posterodorsal to it, rather than a rigid upper lip. The mouth of *N. americana* is unfortunately not known.

The gonopore-anus was to the left of the tail in *P. menevensis*, between plates i and j. This was very similar to the situation in *Cothurnocystis elizae* and '*C.*' *fellinensis* and differed strikingly from that in *Ceratocystis perneri* where the gonopore and anus were right of the tail and sometimes, though not always, slightly separated from each other. As discussed below, *C. perneri* probably represented the primitive condition in these respects. When the gonopore-anus was to the left of the tail it lay in the outwash from the branchial slits, so that faeces and gametes would have been flushed away (Jefferies 1986, Ch. 7). This was presumably advantageous. As in most cornutes, a gonorectal groove in *P. menevensis* ran inside the head (Pl. 54, fig. 4; Pl. 55, fig. 3; Pl. 60, figs. 3, 9, 10) across the floor of the posterior coelom from the gonopore-anus to right of the tail, i.e. to the place where these openings were situated in *C. perneri*. In *N. americana* the gonopore-anus was probably to the left of the tail, for the right part of a gonorectal groove can be seen in the only known specimen and is disposed as in *Cothurnocystis elizae* and most other cornutes. However, the specimen is too damaged to prove the existence of a gonopore-anus between plates i and j.

There was almost certainly no hydropore in *P. menevensis*. This opening existed in *Ceratocystis perneri* where it was a slit crossing the suture of plates f and h. In *P. menevensis* there was no such suture, for plate f did not contact plate h, but the suture of plates f and g had a corresponding position in the head and had no such notch (Pl. 57, fig. 4). It is theoretically possible that a hydropore existed and emerged in the dorsal integument, but this is unlikely since some sort of special organization for it would, in that case, be expected. *C. perneri* is the only cornute known to have had a hydropore, and by outgroup comparison with echinoderms, this is a primitive condition. The absence of a hydropore is an advanced condition and a synapomorphy of *P. menevensis* with all cornutes other than *C. perneri*, with mitrates, and with all other crown-group chordates (including those still extant).

The branchial slits of *P. menevensis* were almost certainly situated just to the left of the tail, in the posterior patch of plated integument, but were not well-defined skeletally. Indeed, the most obvious signs of them are half-moon shaped plates, at least three in number, each of which probably represents the posterior U-plate of a slit (pu in text-fig. 15, cf. Pl. 54, fig. 1). There is space, however, for several other such plates in the specimens. Unlike *N. americana*, there is no definite sign in *P. menevensis* of U-plates framing the slits anteriorly and it may be, as shown in the reconstruction (text-fig. 10), that each slit merely slightly notched the integument anterodorsal to it (this integument is shown in Pl. 54, fig. 1). Comparison with *C. perneri* suggests that the integument anterodorsal to the slits was evolved by the breakup of plate 1, which formed the dorsal margin of all seven slits in *C. perneri*. It is no surprise that the posterior U-plates of *P. menevensis* were differentiated while anterior U-plates were not (or not clearly), since three of the seven gill slits of *C. perneri* had posterior U-plates while none had anterior U-plates. The presumed position of the gill slits of *P. menevensis* is of interest—they would all be posterior to the gentle ridge which ran from plate 2, along plates 1_1, 1_2, and 1_3 to the keel on plate k. This was different from *C. perneri* where two of the slits were anterior to the ridge and only five lay behind it.

Figs. 1–4. *Protocystites menevensis* Hicks. Latexes, all from loc. 2, Porth-y-rhaw (see text-fig. 7). 1, BM(NH) E63022, stylocone and hind-tail ossicles in dorsal aspect; the ossicle marked ! is seen in anterior or posterior aspect and indicates the original shape in transverse section, × 10·8; crf, crescentic facet; mg, median groove; stc, stylocone; tg, transverse groove. 2 and 3, BM(NH) E62958, a single plate b in dorsal and ventral aspects, × 5·2 and × 8·2 respectively. 4, BM(NH) E62958, a different plate b in ventral aspect, × 4·3.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.

PLATE 59

JEFFERIES, LEWIS and DONOVAN, *Protocystites*
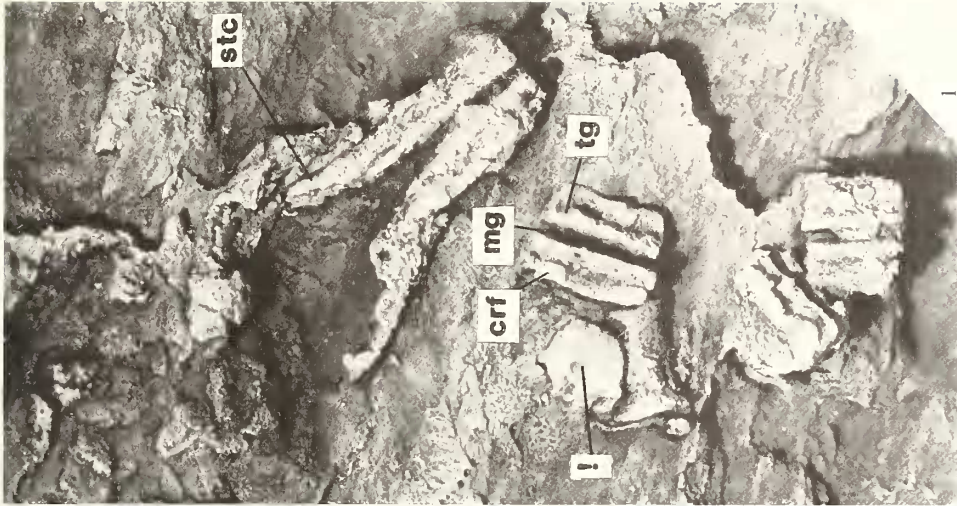
The dorsal groove, which in life probably contained a median eye, was situated in plate y (dg in Pl. 58, fig. 2), at the summit of the dorsal arch of the tail insertion. It is identified as having contained a median eye by comparison with *C. perneri* where it arose in the mid-line from the dorsal face of the brain (i.e. from a region identified as optic by comparison with mitrates and through them with fish; see Jefferies 1986, Chs. 7 and 8) and went up to the dorsal surface of the head where it could readily receive light (Jefferies 1969, p. 521). This eye cannot be homologous with either of the median eyes of modern vertebrates (epiphysis, paraphysis). For these occur only within the monophyletic group of the myopterygians (lampreys + gnathostomes) whereas no median eye exists in: 1, crownward cornutes, e.g. *Corthurnocystis elizae*, *Scotiaecystis curvata* Bather, 1913, and the series of plesions leading crownward of these forms to the mitrates, i.e. *Galliaecystis*, *Amygdalotheca*, *Reticulocarpos hanusi*, and *R. pissotensis* Chauvel and Nion, 1977; 2, the mitrates which were primitive crown chordates and therefore included the latest common ancestor of living chordates; and 3, the myxinoids, which are the living sister group of the myopterygians. The situation of the dorsal groove of *P. menevensis*, notching the ventral edge of plate y, is fundamentally like that of *Ceratocystis perneri* and even more similar, in the small size of plate y, to '*Cothurnocystis*' *fellinensis* and some other cornutes such as *Phyllocystis blayaci* Thoral, 1935, *P. crassimarginata* (Thoral, 1935), and *Chauvelicystis ubaghsi* (Chauvel, 1966) (see Ubaghs 1969). Among known cornutes the presence of plate y with a dorsal groove is certainly a primitive feature.

The narrow groove (ear) of *Protocystites menevensis* is anomalous in some ways. In the one specimen where it has been seen (text-fig. 16; Pl. 55, figs. 1 and 2), it is grossly in the same position as that of *Ceratocystis perneri*, penetrating the posterior wall of the head to the left of the tail. These two cornutes are the only species known to possess such an opening. It seems highly probable that the openings are homologous in both species and, for reasons explained by Jefferies (1986, Ch. 7) with reference to *C. perneri*, that they represent the primitive beginnings of the acustico-lateralis system—or, more precisely, they contained an ear functioning as lateral line. The exact position of the ear of *P. menevensis* is remarkable, however, for it penetrates plate j dorsal to the keel of this plate (Pl. 55, figs. 1 and 2), whereas in *C. perneri* it penetrates plate i ventral to the equivalent keel (which is on plate i) and just dorsal to plate j (text-fig. 11c; Jefferies 1969, pl. 95, fig. 1; pl. 96, fig. 10). Although *C. perneri* and *P. menevensis* were the only known cornutes with a narrow groove, it is likely that all cornutes had an ear, for there is evidence of a homologous ear in mitrates (Jefferies 1969, p. 521; 1986, Ch. 8). Probably the ear in most cornutes had become undetectable in the fossils by being conflated with the gonopore-anus. If the gonopore-anus in *C. perneri* is imagined to move from left of the tail to right of the tail, to take up a position between plates i and j as in other cornutes, then the narrow groove would come to be situated in the ventral part of the gonopore-anus. But the narrow groove in *P. menevensis* was separated from the gonopore-anus and is therefore different, not only from that of *C. perneri*, but probably also from that of the ear in all other known cornutes. The fact that the ear is not conflated with the gonopore-anus is therefore a primitive resemblance to *C. perneri*, but its exact position is likely to be a specialization of *P. menevensis* alone.

Flexibility in the heads of Protocystites menevensis, Ceratocystis perneri, *and* Nevadaecystis americana. *C. perneri* (text-fig. 11) shows some signs of flexibility between some of the plates of the head. These signs are of two types: accessory gaps and transversely rounded plate contacts. The accessory gaps are small irregular

Figs. 1–10. *Protocystites menevensis* Hicks. Isolated plates, all from loc. 2, Porth-y-rhaw (see text-fig. 7). 1 and 2, BM(NH) E63013, latexes of plate k in posteroventral and posterodorsal aspect respectively, both × 4·1; ksp, k-spike. 3 and 4, BM(NH) E62952, latexes of a plate g in dorsal and ventral aspects to show the irregularly disposed ribs in the anterior part of the plate, × 3·9; cb, cerebral basin; oesf, oesophageal fold; pc, posterior coelom; pr, process separating right anterior coelom from posterior coelom (equivalent to cleft in fig. 9, etc.); pvl, pharyngo-visceral line. 5–7, BM(NH) E62958, all showing the same plate; 5 and 6, latexes in ventral and dorsal aspect; 7, natural mould in ventral aspect (cf. Pl. 57, fig. 4), all × 8·7; int, intestine; sto, stomach; pw, pharyngeal wall; pvl, pharyngo-visceral line. 8, BM(NH) E62958, latex of plate l in ventral aspect (same plate as Pl. 58, fig. 3), × 4·6; lsp, l-spike; rs, retiform stereom. 9 and 10, BM(NH) E63034, a plate g as natural mould in ventral aspect and as corresponding latex in dorsal aspect, both × 5·6; br, brain; cl, cleft between posterior coelom and right anterior coelom; gr, gonoduct-rectum; oes, oesophagus; pc, posterior coelom; st, change in stereom from almost imperforate at right posterior to thin and retiform at left anterior.

When not otherwise explained, isolated letters and numbers are the notations of plates (see text-fig. 10); all figs. whitened with ammonium chloride sublimate.

PLATE 60
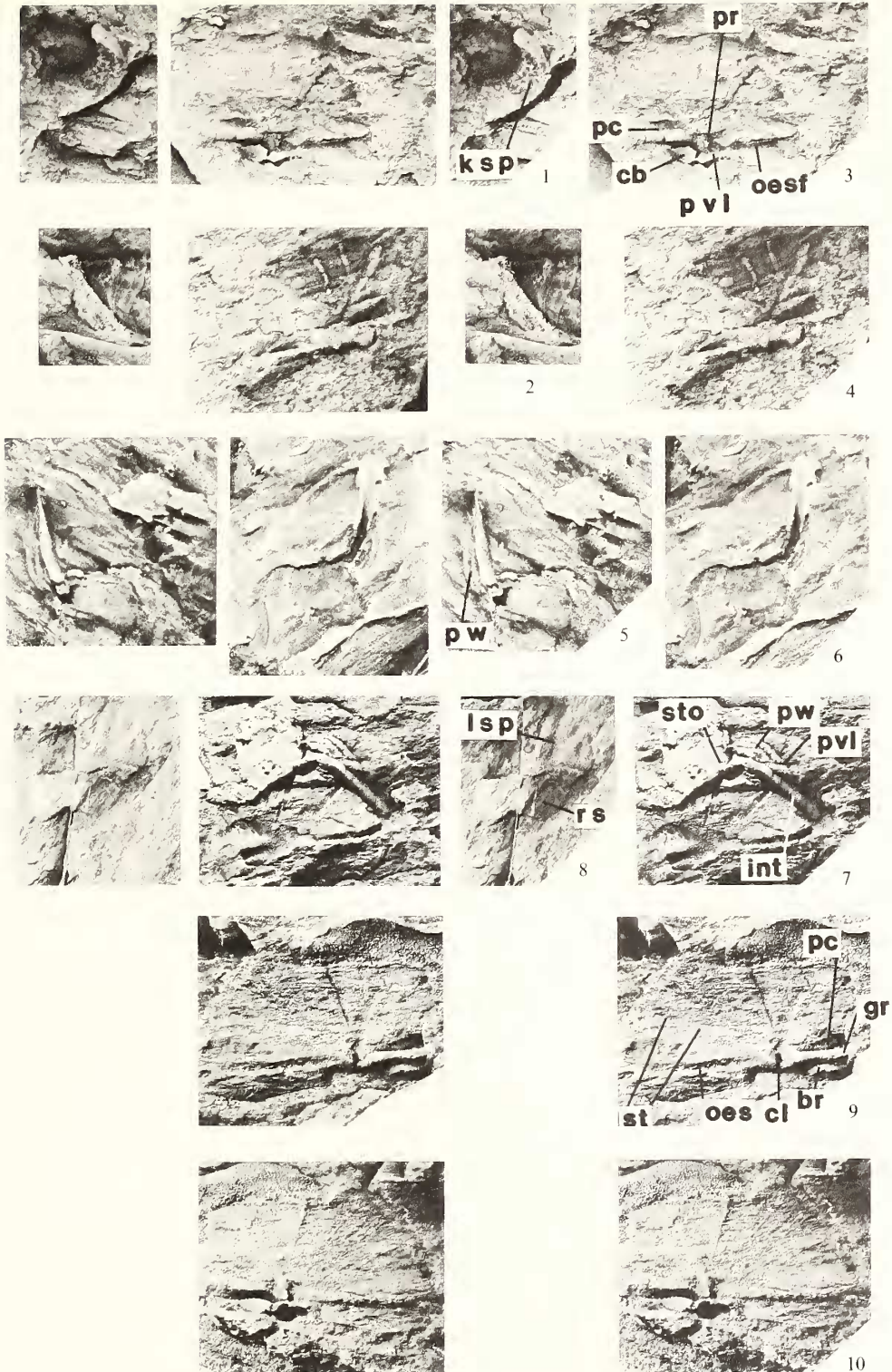
voids situated along the dorsal margins of plates k and l (at their junctions with plates u and l) and along the ventral (or posterior) margins of the three posterior branchial U-plates, where these joined plates k, i, and y. The accessory gaps were therefore situated at the edges of areas which in *P. menevensis* were flexible, i.e. the left anterior integument and the integument posteroventral to the gill slits. This in turn suggests that the accessory gaps in *C. perneri* represented the beginnings of flexibility in the head—meaning, in this species, the ability slightly to raise and lower the roof.

Transversely rounded plate contacts in *C. perneri* occurred near the right side of the head, along the contacts of plates e and f, plates 5 and e, and plates c and d (text-fig. 11*b*). The most striking was that between plate 5, whose ventral edge was convexly cylindrical, and plate e, whose dorsal edge was concave to receive the opposed cylindrical edge of plate 5. These cylindrically rounded plate contacts were almost continuous with each other in *C. perneri* and would have formed a sort of hinge line near the right side of the head—a line along which minimal rotation would have allowed the roof to be raised or depressed slightly. In *P. menevensis* the dorsal border of plate e made contact partly with integument and partly with centrodorsal plate 5 (text-fig. 15; Pl. 54, figs. 1 and 3). The right integument of *P. menevensis*, being flexible, could presumably inflate and deflate; in this motion, plate 5 would rotate about its contact with plate e, exactly as deduced for *C. perneri* but probably to a greater extent. This situation in *P. menevensis* therefore tends to confirm that the supposed right hinge line of *C. perneri* indeed acted as such. The rest of the right hinge line of *C. perneri*, however, does not seem to have been specially flexible in *P. menevensis*, so far as can be deduced from the ill-preserved fossils. Rather the line of flexibility between plates 5 and e would have passed forward between plates 3 and c and rearward between the dorsal integument and the dorsal edge of plate f. To sum up, signs of slight flexibility between the head plates of *C. perneri* largely correspond to signs of greater flexibility in *P. menevensis*, but there are exceptions where the correspondence does not hold.

The dorsal surface of *N. americana* (text-fig. 12), though not completely known, seems to have been more flexible than that of *P. menevensis*. Thus neither plate 3 nor plate 5 is definitely recognizable, presumably being represented by plates of the dorsal integument of the right side of the head. Plate ü is represented by three adjacent plates, not by one, or perhaps two, as in *P. menevensis*. On the other hand, plate 6 of *N. americana* is larger and more recognizable than that of *P. menevensis*. Indeed, it is possible that the plate labelled 2 in *P. menevensis* is in fact equivalent to 2 + 6 of *C. perneri* and *N. americana*. Concerning the dorsal integument in the left part of the head in *N. americana*, there is little direct evidence. However, there is a three-rayed keel on plate 2 and the left posterior ray of this keel points towards the left extremity of the head. Perhaps this ray, as in *P. menevensis*, was continued leftward by a line of keeled plates disposed anterior to the gill slits (though no such plates are preserved in the only known specimen). Unlike *P. menevensis*, such a crest cannot have led to plate k, which is entirely posterior to the gill slits in *N. americana* and carries no crest. To sum up, *N. americana* has the same three dorsal integuments as in *P. menevensis* (1, right; 2, posterior; 3, left anterior), and these three integuments are larger relative to the individualized dorsal plates. It is possible that the left anterior integument of *N. americana*, unlike *P. menevensis*, was not entirely separate from the posterior integument.

The chambers and soft anatomy of the head. Considering cornutes as a whole, there is direct evidence for four chambers in the head, and presumptive comparative evidence for a fifth (Jefferies 1986, Ch. 7). The chambers for which there is direct evidence were the buccal cavity, the right anterior coelom, the posterior coelom, and the pharynx (left or primary pharynx) (text-figs. 20–22). The chamber for which the evidence is purely comparative is the left anterior coelom. The evidence for these chambers is different in different cornutes but they probably all existed in all of them. A modification of the cornute arrangement occurred in mitrates, but differed in several ways, chiefly in the existence of a right pharynx, with right gill slits, as well as a left pharynx.

The evidence for these head chambers in cornutes can be exemplified from *Cothurnocystis elizae* (text-fig. 20). (For a complete discussion, see Jefferies 1986, Ch. 7.) In this species the buccal cavity filled the 'ankle' part (buccal lobe) of the boot-shaped head, immediately behind the mouth. It is defined posteriorly on the right by a vertical ridge on the inside face of plate e and posteriorly on the left by the right-angle bend in plate a which delimits the buccal lobe or, in one specimen, by a vertical ridge on the inside face of plate a just anterior to that bend. In middle-sized specimens of *C. elizae* there is also a difference in the plates of the dorsal integument as between the buccal cavity and regions posterior to it: over the buccal cavity, the plates are polygonal without gaps between them, whereas behind the buccal cavity, over the pharynx, the plates are circular and separated by gaps—perhaps suggesting, if there were muscles in the gaps, that the dorsal wall of the pharynx was more muscular than that of the buccal cavity. The posterior coelom in *C. elizae* was a small, approximately hemispherical chamber just anterior to the tail and convex anteriorly. It was defined
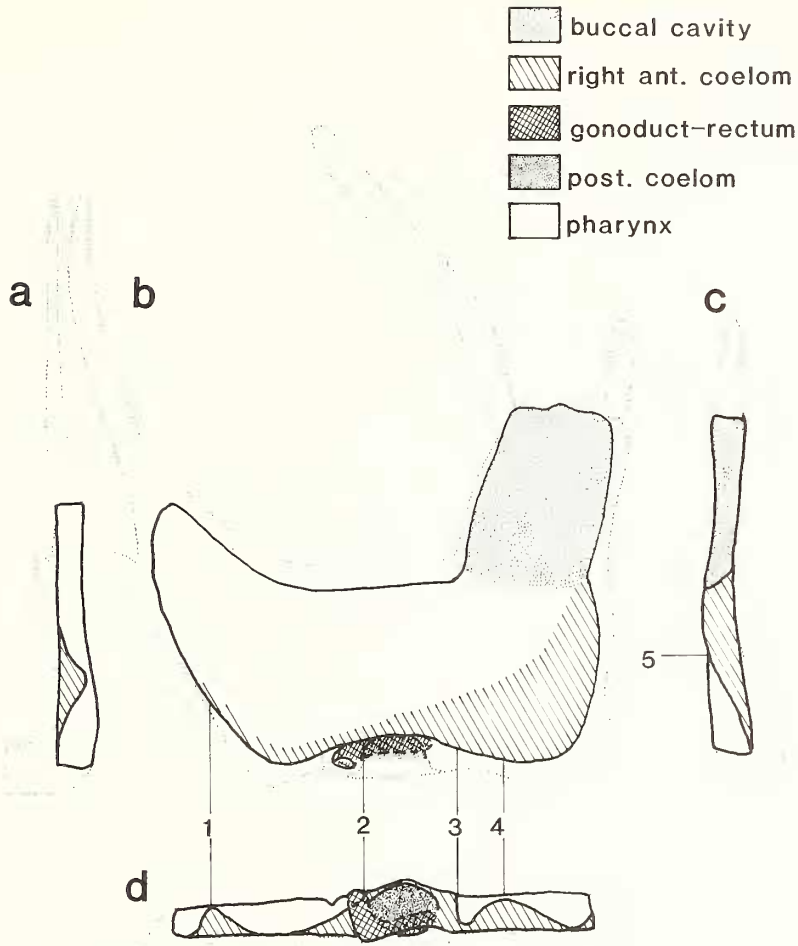
TEXT-FIG. 20. *Cothurnocystis elizae* Bather; the chambers of the head (redrawn after Jefferies 1968, text-fig. 4). 1–5 are the high points of the pharyngo-visceral line. *a*, left lateral; *b*, dorsal; *c*, right; and *d*, posterior aspects.

anteroventrally by an anteriorly convex ridge on the upper, interior surface of plates g and j and would have made contact anterodorsally with the concave posteroventral surfaces of plates h and i. A gonorectal groove, indicating the position of gonoduct and rectum, traversed the floor of the posterior coelom from right to left and climbed vertically upwards near its end to finish at the gonopore-anus to the left of the tail. The posterior coelom was homologous with the left epicardium of tunicates (Jefferies, in press, Ch. 7 and 8).

In the 'foot' part of the boot in *C. elizae*, there is direct evidence for two further chambers, one overlying the other. The upper chamber is characterized in the larger specimens by a special ornament on the internal surfaces of the marginal plates: a decussate ornament of strong horizontal lines crossed by weak vertical ones. The branchial slits opened through the roof of this chamber, so it can be identified as the pharynx. The lower chamber was mainly situated in the posterior right corner of the head and is characterized by the smooth surface of the stereom where the chamber made contact with the inside faces of the marginal plates. A sharp but undulating line (the pharyngo-visceral line) separated the smooth areas from the overlying ones of decussate pharyngeal sculpture. The undulations of the pharyngo-visceral line are the same in different specimens, and there are five high points where it made contact, or almost so, with the upper edge of the
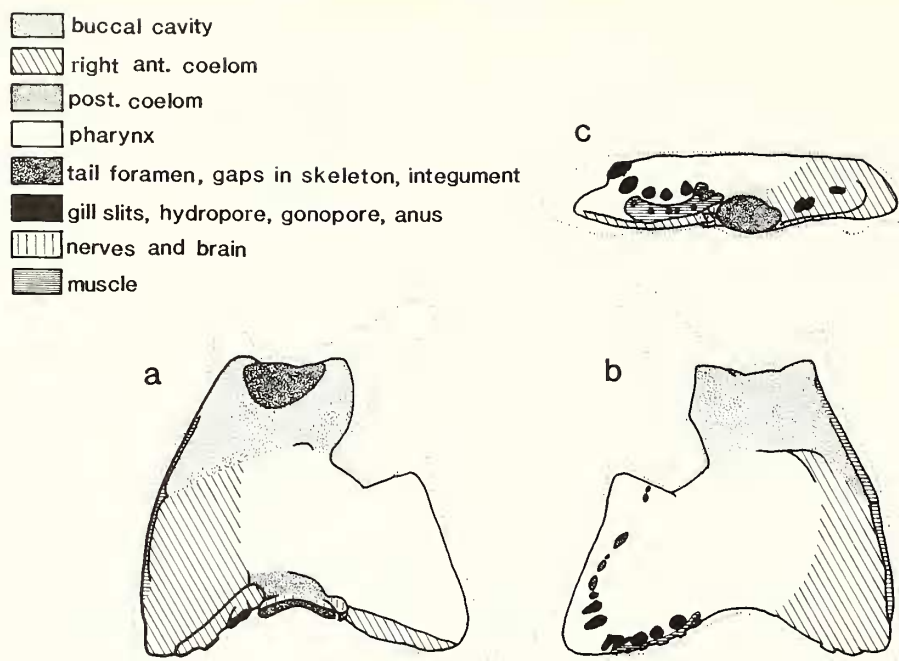
TEXT-FIG. 21. *Ceratocystis perneri* Jaekel; the chambers and other soft parts of the head (redrawn after Jefferies 1969, text-fig. 10). *a*, ventral; *b*, dorsal; and *c*, posterior aspects.

marginal plates. These points are numbered 1 to 5 from left to right. The gonorectal groove, which passes under the posterior coelom, emerges on the right from the lower chamber and approaches the posterior coelom from anterior right. If the groove indeed carried the gonoduct and rectum, then the non-pharyngeal gut (except the rectum) and the gonad were situated in this lower chamber, which therefore functioned as coelom; we call it the right anterior coelom.

The fifth chamber in *C. elizae*, for which there is only comparative evidence, can be called the left anterior coelom. It probably overlay the pharynx and buccal cavity and would probably have been virtual (i.e. with no open cavity). It corresponds to the left somatocoel of echinoderms (which faces upwards in crinoids), the left mandibular somite of vertebrates and acraniates, and the left metacoel of hemichordates. Once again, the arguments for its existence can be found in Jefferies (1986, Chs. 7 and 8).

The same chambers probably also existed in *Ceratocystis perneri* (text-fig. 21). Here again, there is direct evidence for buccal cavity, right anterior coelom, posterior coelom, and pharynx; and the left anterior coelom is presumed to have existed. The main differences in the head chambers between *C. perneri* and *Cothurnocystis elizae* were: 1, in *Ceratocystis perneri* the right anterior coelom was extensively in contact with the right side of the head, whereas in *Cothurnocystis elizae*, so far as is determinable, it made contact only with the right and posterior faces of the marginals; 2, in *Ceratocystis perneri* the hydropore, gonopore, and anus opened direct from the cavity of the right anterior coelom, passing through the posterior wall of the head to the right of the tail, whereas in *Cothurnocystis elizae* there was no hydropore and the gonopore-anus was to the left of the tail, connected with the right anterior coelom by gonoduct and rectum which traversed the floor of the posterior coelom (as indicated by the gonorectal groove).

In *P. menevensis* the same chambers probably existed as in other cornutes. The buccal cavity presumably occupied the 'ankle' part of the boot-shaped head, i.e. the buccal lobe. Its probable right posterior margin was defined by a triangular wedge of callus on the internal face of plate e (pbbc in text-fig. 15, cf. Pl. 54, figs. 1 and 3; text-fig. 17 and Pl. 54, fig. 1; Pl. 56, fig. 1; Pl. 58, fig. 4), this wedge being comparable in position to the ridge on the internal face of plate e in *C. elizae* and many other cornutes. The posterior coelom was well defined ventrally by a crescentic area on the floor of the head just to the left of the tail. This crescent was concave upwards (pc in Pl. 54, fig. 4; Pl. 55, fig. 3; Pl. 56, fig. 3; Pl. 57, fig. 4; Pl. 58, fig. 4) and floored by
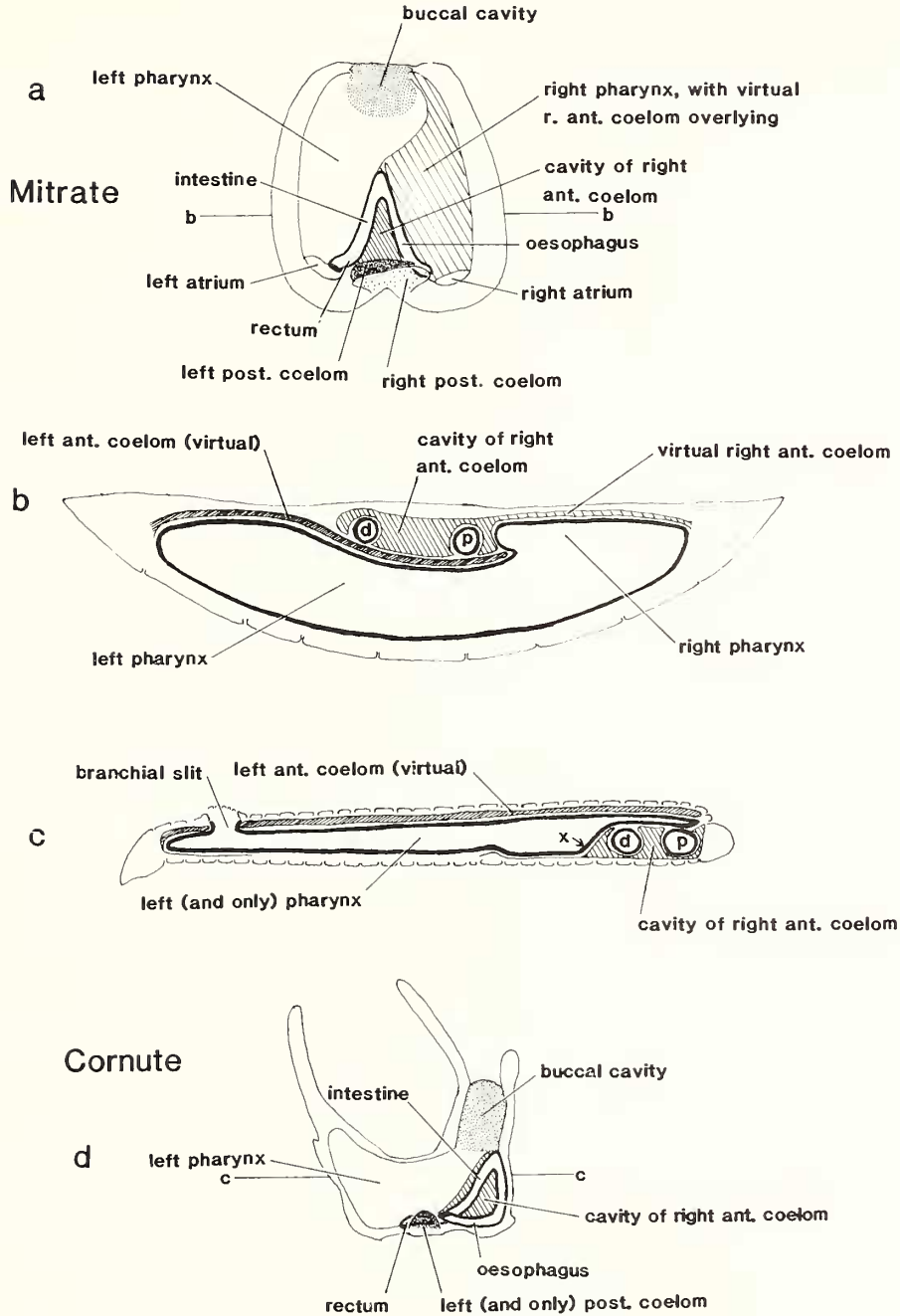
TEXT-FIG. 22. The soft parts of the head in: *a*, *b*, a mitrate (*Mitrocystites*); and *c*, *d*, a cornute (*Cothurnocystis*) (redrawn after Jefferies 1981*a*, fig. 5). *a*, dorsal aspect; *b*, section through b–b of *a*; *c*, section through c–c of *d*; *d*, dorsal aspect. The mitrate condition can be derived from the cornute condition mainly by origination of a right pharynx, which would have appeared at the point x of *c*.
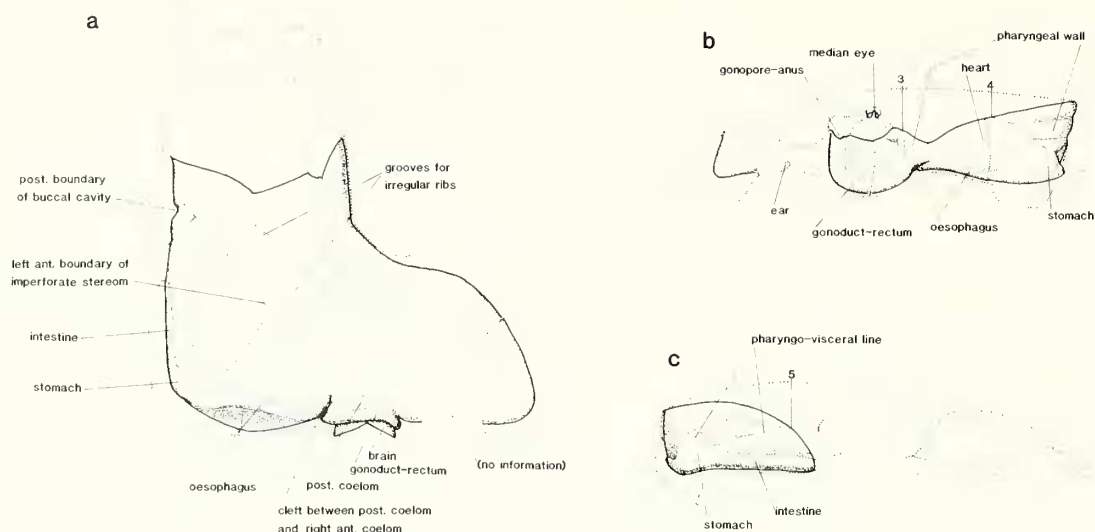
TEXT-FIG. 23. *Protocystites menevensis* Hicks; reconstructed internal natural mould (i.e. soft parts). *a*, ventral; *b*, posterior; and *c*, right lateral aspects. The reconstruction stops arbitrarily at the anterior margins of plates a, e, and x.

almost imperforate stereom (text-fig. 23*a*; Pl. 55, fig. 3), by contrast with the floor anterior to it, which is made of thin, retiform stereom stiffened with ribs. A distinct gonorectal groove crosses the floor of the posterior coelom transversely and climbs upwards to the left of the tail to end at the gonopore-anus (Pl. 56, fig. 3). Thus the gonoduct and rectum would have crossed the floor of the posterior coelom, as in *C. elizae* and all known cornutes except *Ceratocystis perneri* where, as already stated, the gonopore-anus was to the right of the tail. A high wall rising from the floor of the head in plates g and j formed the posterior limit of the posterior coelom (vw in Pl. 54, fig. 4) and separated that chamber from the deduced position of the brain. The latter was situated in a distinct cerebral basin (Pl. 54, figs. 1 and 4; Pl. 60, fig. 3) excavated in plates g and j and faced with almost imperforate stereom. In having such a basin, with a high wall in front of it, *P. menevensis* once again differed from *C. perneri* and resembled more crownward cornutes such as *Cothurnocystis elizae*. Anterodorsally, the limit of the posterior coelom presumably coincided with the posteroventral surfaces of plates h, y, and i, but these surfaces have not been seen in the available specimens.

Regarding the chambers in the remainder of the head—behind the buccal cavity but in front of the posterior coelom—*P. menevensis*, like other cornutes, probably had a pharynx overlying a right anterior coelom, with the latter lying mainly in the posterior right portion of the head. As to the evidence, in the posterior wall and right wall of the head, on the inside faces of plates g and f, a clear pharyngo-visceral line is visible (text-fig. 23*c*; pvl in Pl. 57, fig. 4; Pl. 60, figs. 3, 6, 7). This line separates a smooth, almost imperforate, surface below, with a thick wall of stereom, from retiform stereom above, forming a very thin wall. Indeed, in the anterior part of plate f the stereom above the line is not merely retiform but thrown into horizontal folds, like those in the pharyngeal ornament of *C. elizae*. Moreover, the wall of plate f is so thin above the line in this region that the folds are visible from outside, and thus the pharyngo-visceral line can be detected externally (text-fig. 10*d*; pw in Pl. 60, fig. 5). Also, the undulations of the line in the right part of the head are the same as in *C. elizae* with high points 3, 4, and 5 clearly recognizable. It is reasonable to suppose that, as with *C. elizae*, the marginal plates were in contact with the pharynx above the pharyngo-visceral line (or rather with virtual left anterior coelom embracing the pharynx) and with right anterior coelom beneath it. Moreover, the left boundary of the right anterior coelom, or at least the cavity of that coelom, is indicated in *P. menevensis* by a change in the stereom in the floor of the head. Thus, in the right posterior portion of the head, in plates f and é (Pl. 54, fig. 1), in the posterior right parts of plates g (Pl. 55, fig. 3; Pl. 60, fig. 9) and a (Pl. 56, fig. 1, for the internal surface of the plate; Pl. 55, fig. 1 for the external surface), and in the right posterior part of plate e,
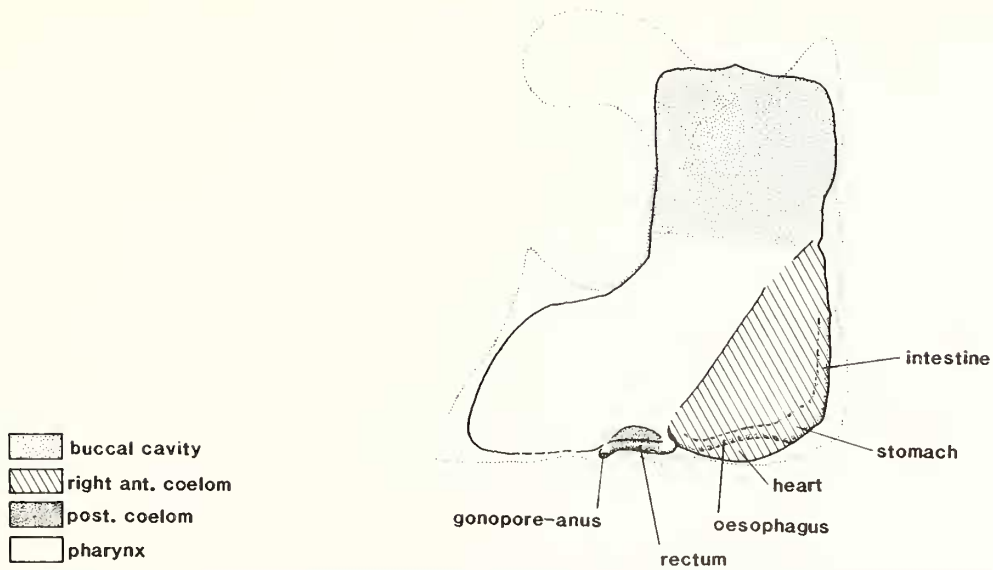
TEXT-FIG. 24. *Protocystites menevensis* Hicks; the chambers and other soft parts of the head in dorsal aspect.

the upper surface of the floor of the head is constructed of almost imperforate stereom, continuous with that below the pharyngo-visceral line in the right and right posterior wall of the head. The left anterior limit of such stereom is a line running forwards and rightwards from near the right side of the tail insertion (text-fig. 23a); and to the anterior left of this line, the floor stereom is of different nature being thin and retiform, except where it is thickened by ribs (space-frame construction). The region of almost imperforate stereom, whether in the floor or in the posterior faces of the posterior and right walls below the pharyngo-visceral line, was probably in contact with the right anterior coelom and indicates the extent of that chamber. The rest of the floor of the head, left of the area of almost imperforate stereom, was presumably overlain by pharynx, though perhaps there was, beneath the pharynx but above the stereom, a purely virtual extension of right or left anterior coeloms in this region. The pharynx would also have made contact with the posterior and right walls of the head dorsal to the pharyngo-visceral line (though again it would probably have been clothed with virtual left anterior coelom). As in other cornutes, the branchial slits, just to the left of the tail insertion, would penetrate the roof of the pharynx.

The pharyngo-visceral line cannot be traced to the left of the tail insertion. This is because no known specimens show the internal face of the left part of plate j.

A process on the internal surface of plate g, and a corresponding cleft in the natural mould (text-fig. 23a; Pl. 55, fig. 3; Pl. 60, figs. 3, 9, 10), is situated between the deduced positions of the posterior coelom and the right anterior coelom. It varies in shape, but tends to be anteroposteriorly elongate. Probably this process was intercameral and represented the stereomic infilling of a gap between the limiting epithelia of the posterior and right anterior coeloms. As already mentioned, this process is situated in a position corresponding to the posterior end of the strut in cornutes more crownward than *P. menevensis*. It may represent the evolutionary beginnings of the strut.

The left anterior coelom probably covered the whole of the dorsal surface of the pharynx in *P. menevensis* but had no cavity, being solely virtual. As with other cornutes, and also with mitrates, the arguments for its existence are purely comparative.

As to the contents of the right anterior coelom, the most direct evidence comes from *Ceratocystis perneri*, where the hydropore, gonopore, and anus opened directly out of it. In that species, therefore, the right anterior coelom is likely to have contained the non-pharyngeal gut, the gonad, and whatever organs were associated with the hydropore. Among the latter, the heart and pericardium were probably included for the pulsatile madreporic vesicle (pericardium) and the contained head process of the axial organ (heart) are situated near the hydropore in living echinoderms. Important evidence as to the contents of the right anterior coelom comes

also from mitrates such as *Placocystites forbesianus* (Jefferies and Lewis, 1978) (Jefferies 1986, Ch. 8). In mitrates, however, the position of the right anterior coelom, hanging from the ceiling of the head near the mid-line, is governed by the right pharynx which in cornutes did not exist. Clear signs indicate that the oesophagus of mitrates opened from the right posterior coelom into the pharynx to the right of the mid-line, near the posterior right corner of the cavity of the right anterior coelom (as shown in text-fig. 22a). From here, the non-pharyngeal gut ran forward to an unknown extent, along the right margin of the cavity of the right anterior coelom, turned through an angle, and ran rearwards along the left margin of this cavity to join the rectum, which debouched into the left atrium. The gonad was probably situated in this loop of the gut, partly because the gonoduct seems to arise from this position in the mitrate *Mitrocystella*, and partly because the gonad is situated in the loop of the gut in enterogonous tunicates. The contents of the right anterior coelom of mitrates is further discussed by Jefferies (1986, Ch. 8).

The cornute condition of the right anterior coelom can partly be deduced by mentally subtracting the right pharynx from the mitrate condition, reversing what happened in evolutionary history. This would allow the cavity and contents of the right anterior coelom to fall to the floor of the head and to occupy the posterior right portion of the head, as seems to have been true in *C. perneri*, *Cothurnocystis elizae*, *Protocystites menevensis*, and other cornutes. In that case, the non-pharyngeal gut would follow the periphery of the cavity of the right anterior coelom (as suggested in text-fig. 22d). Part of the intestine would run leftwards and rearwards along the left margin of the cavity to join the rectum in the posterior coelom. (There is direct evidence in *C. elizae* that the intestine approached the rectum by running leftwards and posteriorly, but in *P. menevensis* the internal moulds indicate that it probably joined the rectum by running almost vertically downwards.) And the oesophagus of cornutes would run rightwards, from a position to the right of the tail insertion, just in contact with the right posterior wall of the head.

Some direct indication of the non-pharyngeal gut inside the right anterior coelom of *P. menevensis* is probably given by the internal sculpture of plates g and f. As already mentioned, a distinct fold in plate g, concave upwards and convex downwards (Pl. 55, fig. 3; Pl. 60, figs. 3, 9, 10) and corresponding to a horizontal hemicylinder on the surface of the natural mould, runs rightwards into plate f (Pl. 55, fig. 4) and coincides with the position of the oesophagus as reconstructed above for cornutes in general; we assume that the fold carried the oesophagus and therefore call it the oesophageal fold. This fold is ventral to high point 4 of the pharyngo-visceral line but makes up only a small portion of the internal surface beneath that high point. Some other organ, as discussed later, presumably filled the area between the oesophageal fold and the pharyngo-visceral line. More anteriorly, in the right wall of plate f (Pl. 57, fig. 4; Pl. 60, figs. 6 and 7), the pharyngo-visceral line ascends towards high point 5. On the internal natural moulds, however, the surface beneath this line is complex in this region. Ventrally the natural mould formed a horizontal hemicylinder whose upper edge was distinct from, and much more ventral than, the pharyngo-visceral line and whose radius was about the same as that suggested for the oesophagus by the oesophageal fold. This hemicylinder corresponds to a groove on the inner face of plate f and presumably it too carried a portion of the gut. More posteriorly, just anterior to the right posterior angle of the head, the hemicylinder expands into something more inflated. This inflation may represent the stomach (Pl. 57, fig. 4; Pl. 60, fig. 7), in which case the gut anterior to it would be part of the intestine.

The organ beneath high point 4 but dorsal to the presumed oesophagus may have been the pericardium and heart. This conclusion, which is highly tentative, is based on two opposite approaches. First, the position roughly coincides with that of the hydropore in *Ceratocystis perneri*; and the heart and pericardium of echinoderms (head process of axial gland and madreporic vesicle) are located just internal to the hydropore. Secondly, the heart of tunicates is located on the right side of the gut, as may have been true of mitrates also. If so, then mental subtraction of the right pharynx to yield the cornute condition would bring the heart against the right posterior wall of the head, next to the oesophagus, to occupy the observed space above the oesophageal fold but beneath high point 4. We believe that the grounds for placing the heart, gonad, and non-pharyngeal gut somewhere inside the right anterior coelom are reasonably strong. The reasons for putting them in particular grooves and depressions in the inner face of the skeleton are necessarily weaker.

Not much can be said about the brain and cranial nerves of *P. menevensis*. The brain, as already mentioned, would have occupied a well-defined cerebral basin excavated in plates g and j (Pl. 54, fig. 1; Pl. 55, fig. 3; Pl. 60, figs. 9 and 10) and faced with almost imperforate stereom. This basin formed part of the posterior surface of the wall that stood behind the posterior coelom. The brain would have extended upwards into the median eye (occupying the dorsal groove) in the posterior surface of plate y (Pl. 58, fig. 2). The left and right pyriform bodies (trigeminal ganglia), which were present in all other cornutes just anterior to the brain, could not be located in *P. menevensis*. If they existed, they either made no contact with the skeleton or else the specimens are too crumpled to show them.

The tail. The tail of *P. menevensis*, like that of all other cornutes, is divided into fore, mid, and hind regions. In text-fig. 10 it is shown as small and slender relative to the head, when compared with *Cothurnocystis elizae* or *Ceratocystis perneri*, for instance. This may be correct but, because of tectonic distortion, it is impossible to be sure. The abrupt end of the tail is usual, or perhaps universal, in cornutes and mitrates, and in general probably means that more distal segments were regularly lost by autotomy, perhaps several times in the life of the animal. In *P. menevensis*, however, none of the observed tails is well enough preserved to show how it terminated. The reconstruction of the fore tail was particularly difficult, for its dorsal surface is not shown adequately by any specimen.

The skeleton of the hind tail consisted of a median series of ventral ossicles, approximately hemicylindrical in shape, and dorsal plates arranged in right and left series (Pl. 56, figs. 1, 2, 4, 5; Pl. 57, figs. 1 and 2; Pl. 59, fig. 1). So far as can be judged, the plates were not opposite each other on the right and left. Neither were they uniformly related to the ventral ossicles beneath them: the number of plates in the left and the right series, as indicated in particular by the repetition of segmental structures on the dorsal surface of the ossicles, is greater than the number of ossicles, i.e. there is somewhat more than one plate per ossicle on each side proximally, and about two plates per ossicle on each side distally.

The ossicles in life were probably about as wide as deep, as suggested by a specimen whose longitudinal axis lies perpendicular to the bedding plane (Pl. 59, fig. 1). The dorsal, interior surface of the series of ossicles (Pl. 56, fig. 2; Pl. 59, fig. 1) bore a deep median groove which was rounded V-shaped in transverse section. The walls which formed the right and left sides of the groove were intermittently notched by semicircular transverse grooves, but the notches, like the plates, were not opposite each other, nor uniformly related to the ossicles that bore them. Lateral to each notch was a depression in the dorsal surface of each ossicle, each depression being separated from those more proximal and more distal by a transverse ridge. (Each notch is located near the anterior end of the corresponding depression.) The dorsal surface of the ossicles varied in width, being narrowest at the ridges and widest at the depressions. At the lateral end of each ridge there was a flat crescentic facet, concave outwards, which received the articular process of the corresponding dorsal plate.

The dorsal plates, as seen in the specimens, are usually spread out on the bedding plane on either side of the ossicles, being slightly concave on the original internal surface and slightly convex on the original external surface (Pl. 56, fig. 2; Pl. 57, fig. 2). In our view, the outward spread of the plates is preservational and caused by the explosive release of the gases of putrefaction from the soft tissues of the hind tail after death; and the slightness of curvature of the plates probably results from post-mortem compaction perpendicular to the bedding plane. (Ubaghs, who believes that the plates of cornutes could open outwards in life (1981), would probably dispute both these views.) The plates in text-fig. 25 are reconstructed with greater curvature than observed, on the assumption that the median groove of the ossicles contained the notochord and this, being anti-compressional, would lie in the mechanical neutral axis of the hind tail, and therefore near the centre of the hind tail in transverse section. The deduced curvature of the plates is similar to that seen in *C. perneri*, *N. americana*, or *Cothurnocystis elizae*, for example.

Each dorsal plate consisted of a thick-shelled ventral portion and a thin-shelled dorsal portion. The thin-shelled portions presumably met those of the opposite side of the tail at a median dorsal suture, and the edge of such a plate where it would have met the suture is visible in Plate 56, fig. 2 (ms). However, such a median dorsal contact between the dorsal hind-tail plates of the left and right sides has never been seen in the fossils. As already mentioned, it is unlikely that a plate of the left side was ever exactly opposite one of the right, and vice versa. The thick-shelled part of the plate was formed of labyrinthic stereom externally, and of smooth, almost imperforate, stereom internally. The thin-shelled part of the plate consisted of fibrillar stereom, with the fibres directed approximately parallel to the posterior and anterior edges. The thick-shelled part had a convex posterior outline which formed a ventral lobe, and this lobe overlapped the posterior part of the next plate behind. The external surface of the anterior part of the thick-shelled portion of the plate bore a smooth facet (inter-plate facet) which would have slid against the inside face of the next plate in front. The thin-shelled part of each plate probably slightly overlapped the corresponding part of the next plate behind. The anteroventral angle of each plate was produced medianward into an articular process which made contact in life with the crescentic facet on the ventral ossicle.

Three segmentation series, therefore, seem to have existed in the hind tail: 1, that of the ossicles mid-ventrally; 2, the left series of dorsal half-segments; and 3, the right series of dorsal half-segments. The skeleton of each half-segment contained: 1, a plate with its thin- and thick-shelled portions, ventral lobe, articular process, and inter-plate facet; 2, a depression on the dorsal surface of the ossicles, between two successive transverse ridges; and 3, a transverse groove (notch) leading into that depression from the median groove. Each half-segment would have had corresponding soft parts whose nature will be discussed later. Left and right half-segments were about equal in number, but not opposite each other and had no one-to-one
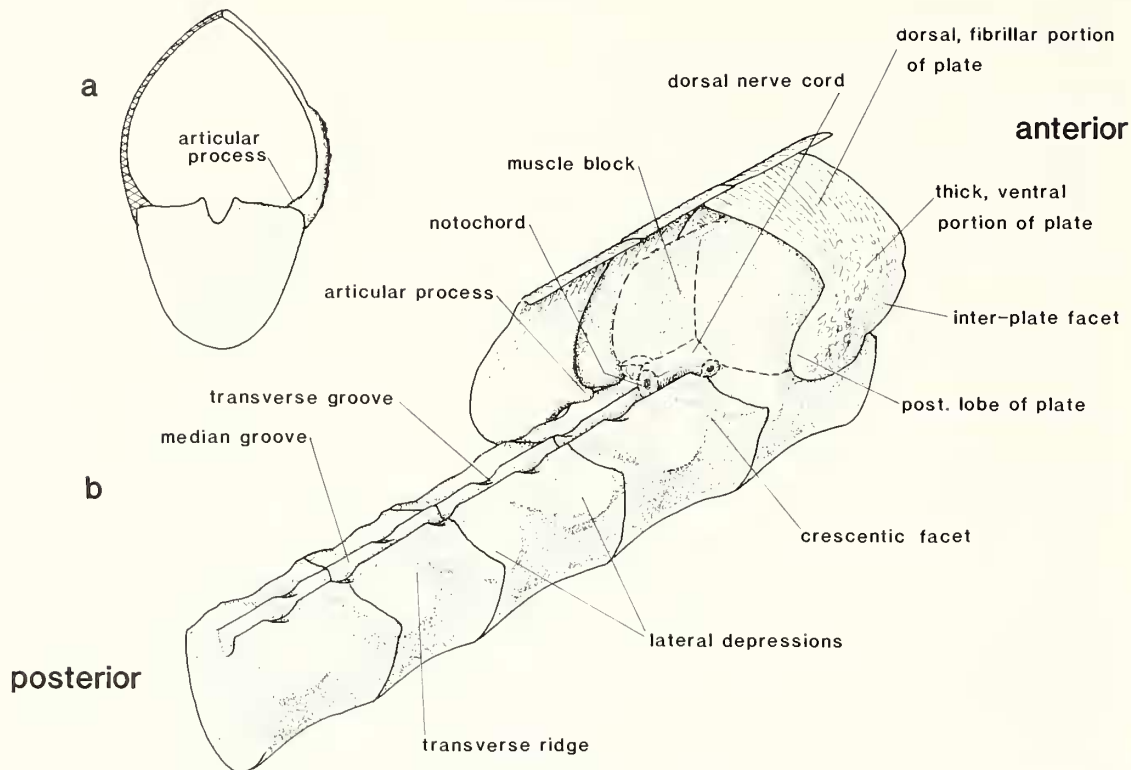
TEXT-FIG. 25. *Protocystites menevensis* Hicks; anatomy of the hind tail. *a*, anterior aspect of a hind-tail ossicle with attached dorsal plates; *b*, posterodorsal aspect of several ossicles and plates. The dorsal nerve cord is shown as overlying the notochord by analogy with the mitrates.

relationship with the ventral ossicles. One specimen suggests that, when the dorsal plates and corresponding soft parts had been lost, the column of ventral ossicles would curve downwards under its own elasticity so as to be concave ventrally (Pl. 56, figs. 4 and 5). This specimen suggests that such would be the relaxed condition of the hind tail during life.

The fore tail would have had a large lumen. The skeleton of the ventral surface of the fore tail can be restored with some confidence (cf. text-fig. 18 and Pl. 57, fig. 1). There were about three ventral plates on the left and right, and these overlapped each other in the ventral mid-line and alternated. A similar alternation occurred in *Ceratocystis perneri* (text-fig. 11*b*) where, however, there were many more half-segments on each side (about seventeen instead of about three). The dorsal surface of the fore tail is much harder to reconstruct. In text-fig. 10 the left and right dorsal series of plates, three plates in each series, are shown and the plates of left and right sides are shown as alternating. All this may have been true, partly by analogy with *C. perneri*, but the relevant specimens are smashed to pieces in this region. One specimen (the lectotype, text-fig. 17 and Pl. 56, fig. 1), however, shows a single reasonably complete dorsal plate, so the reconstruction is plausible. It is clear that, as in other cornutes, the skeleton of the fore tail was looser than that of the mid and hind tails and would have allowed much movement. The mid-ventral alternation of left and right plates suggests that most of the movement was flexion from side to side.

The skeleton of the mid tail consisted of a massive stylocone ventrally (text-fig. 15 and Pl. 56, fig. 1; text-fig. 17 and Pl. 57, fig. 1; Pl. 58, fig. 1; Pl. 59, fig. 1) and presumably there were left and right series of plates dorsally. The stylocone was an approximately conical ossicle with a deep anterior excavation. It was probably serially homologous to several ventral hind-tail ossicles. The dorsal surface of the stylocone has a sculpture much like that of the hind-tail ossicles and there are indications of about three half-segments on each side.

As to soft parts, the lumen of the fore tail was probably largely filled with muscle which, to judge by the

mid-ventral alternation of left and right plates, probably served mainly to swing the tail from side to side. Concentration of muscle in the proximal part of an appendage is efficient because, for a given angle of bending, the muscles require a smaller percentage contraction than if attached more distally, and muscles work most efficiently at small percentage contractions (Gray 1957). To prevent telescoping, some anti-compressional structure in the soft parts of the fore tail would have been required, which suggests that a notochord was present. This notochord would have continued rearwards from the fore tail into the mid and hind tail where it would have occupied the median groove. In the hind tail, however, the notochord would have had no anti-compressional function; rather it would have served, like the string in a bead necklace, to keep the ossicles in alignment. By analogy with mitrates, where there is direct evidence in the fossils, and with all living chordates, the notochord was presumably overlain by a dorsal nerve cord. The transverse grooves (notches) probably represent places where nerves went off from the dorsal nerve cord, and perhaps blood vessels from a longitudinal vessel in the notochord, to more lateral parts of the tail. The imbrication of successive dorsal plates in the hind tail indicates that the tail could have curled upwards. Such curling implies the presence of muscles in the lumen of the hind tail which, on contraction, would have shortened the dorsal side of the tail and so caused flexion. These muscles would have required an antagonist, and this was probably supplied by the elasticity in the ligaments of the column of ventral ossicles which, as already noted, seems to have flexed downwards when relaxed. The presence of serial depressions in the dorsal surface of the ossicles, separated by transverse ridges and supplied by whatever filled the transverse grooves, suggest that these muscles were divided into blocks (somites), each muscle block occupying a depression.

SYSTEMATIC POSITION

Some methodological remarks

Text-fig. 26 is a cladogram of the dexiothetes which lays particular stress on the less crownward cornutes near *P. menevensis*. We regard a cladogram as a phylogeny conventionalized by placing all the known forms under consideration at the ends of branches. The terminal branches of a
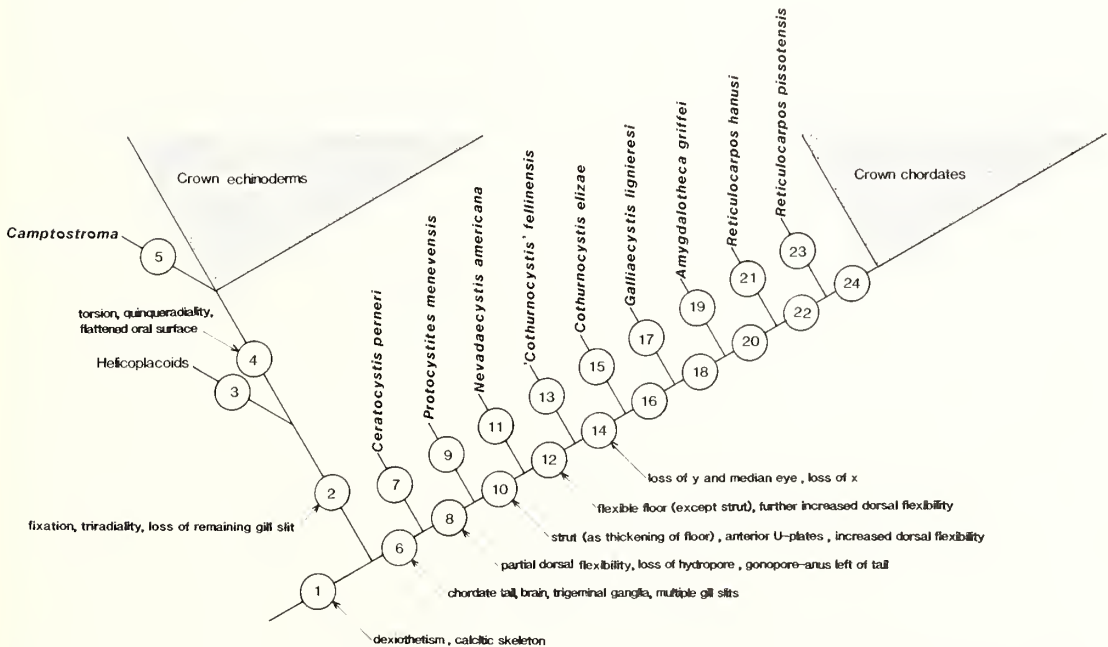
TEXT-FIG. 26. A cladogram of the Dexiothetica to show the position of *Protocystites menevensis* Hicks within the chordate stem group and the origin of some important evolutionary novelties. For fuller explanation see text.

cladogram are therefore in the first place conventional. They can sometimes be shown to have existed, when they did exist, by two types of argument—morphological and stratigraphical. The morphological argument requires that some feature has arisen within the terminal branch, as an autapomorphy of the single species or the species group at the end of the branch. The stratigraphical argument requires, in the present case, that the animal or animals at the end of the branch be contemporaneous with, or preferably later than, their more crownward neighbour. To show that a terminal branch did *not* exist is difficult or impossible. In the present instance this means that, even if the morphological and stratigraphical arguments for the existence of a terminal segment failed, it would be impossible to prove that any known form lay exactly in the chordate stem lineage, in the sequence of even-numbered segments 6–24. Text-fig. 26 is not comprehensive crownward of *N. americana* (segments 12–24) nor anti-crownward of *C. perneri* (segment 6), in the sense that known fossils other than those named belong, or can be suspected of belonging, in those regions. Moreover, the parts of the diagram crownward of *Cothurnocystis elizae* are not discussed in this paper, since they are treated by Jefferies (1986, Chs. 7 and 9).

Particular difficulties arise in establishing the primitiveness of some features of *Ceratocystis perneri*—the least crownward cornute known. When a feature is found in *C. perneri* and also in some related forms, then there is no dilemma. For example, *C. perneri* had a hydropore, uniquely among cornutes; but this feature also occurs in crown echinoderms and in hemichordates (left mesocoel pore), which indicates that it existed in segments 1, 2, 4, 6, and 7 of text-fig. 26 and disappeared within segment 8. Again, *C. perneri* had a rigid floor to the head, and this also existed in *P. menevensis* and *N. americana*; this indicates that a rigid floor existed throughout segments 7–11, in the crownward part of 6, and in the anti-crownward part of 12, and that it disappeared in segment 12. Features unique to *C. perneri* among known forms, however, present difficulties: for prima facie, they could either have arisen in segment 7, as autapomorphies of *C. perneri*, or they could be primitive features of cornutes present throughout segment 7, in the crownward part of segment 6, and in the anti-crownward part of segment 8.

The stratigraphical criterion of primitiveness is of no help in resolving such dilemmas, for the Cambrian record of cornutes it too incomplete, on several grounds. First, only four cornutes have been described from the Cambrian, i.e. *C. perneri*, *P. menevensis*, and the 'stylophoran' of Sprinkle (1976, pl. 1, fig. 1), all of which are approximately contemporaneous and Middle Cambrian in age, and *N. americana* which is Upper Cambrian in age. Secondly, these four forms are considerably different from each other, while *N. americana* from the Upper Cambrian is in most ways intermediate between *P. menevensis* and Sprinkle's 'stylophoran' (which broadly belongs to *Cothurnocystis*) from the Middle Cambrian. Thirdly, new forms are being discovered in the Cambrian (four new species of Cambrian cornute came to our attention in the years 1981 to 1985, one of which is *P. menevensis*). In deciding what features are primitive among Cambrian cornutes, therefore, stratigraphy is useless. (We do not deny that stratigraphy can indicate primitiveness in other groups of fossils (Fortey and Jefferies 1982).)

Functional analysis can sometimes suggest which of two alternative feature states is the more primitive. Thus, in having its gonopore-anus to the right of the tail, *Ceratocystis perneri* was less efficiently laid out than other cornutes, whose gonopore-anus was to the left of the tail and therefore in the branchial outwash, so that faeces and gametes could be flushed away. This suggests: that having the gonopore-anus to the right of the tail was more primitive than the alternative; that this primitive state existed in the crownward part of segment 6 of text-fig. 26, the anti-crownward part of segment 8, and throughout segment 7; and that the change to the location left of the tail happened in segment 8. Such arguments are risky, in as much as functional interpretations are always uncertain.

Anti-crownward extrapolation of an evolutionary trend can also be invoked to indicate that a unique feature of *C. perneri* was primitive. The anti-crownward sequence *Cothurnocystis elizae*, '*C.*' *fellinensis*, *N. americana*, *P. menevensis*, *Ceratocystis perneri* is one of decreasing relationship to the chordate crown group on several grounds. It is also one of decreasing flexibility of the dorsal surface. This suggests that the rigid, or almost rigid, roof to the head seen in *C. perneri*, and only in

it among known cornutes, is the evolutionary starting point from which the flexible roof, seen in increasing degree crownward among other cornutes, developed—essentially in segments 8, 10, 12, and 14 of the chordate stem lineage. However, this argument lacks logical rigour, to the extent that evolution may reverse in direction. It can partly, but not completely, be subsumed as a series of more rigorous sub-arguments in which *C. perneri* is not unique among known forms. For example, *C. perneri* and its crownward neighbour *P. menevensis* are the only known cornutes showing individualized plates 3 and 5 in the roof of the head. If *C. perneri*, because of its hydropore, is the least crownward cornute known, then *P. menevensis* is its crownward neighbour because it retains plates 3 and 5 (among other arguments) and all other cornutes lack these plates as distinguishable elements, presumably having lost them. But sub-arguments of this sort can show only that a condition seen in *P. menevensis* is primitive with respect to all cornutes except *C. perneri*. They cannot show that a condition known uniquely in *C. perneri* is primitive. Anti-crownward extrapolation of evolutionary trends goes further than these sub-arguments, but is less logically rigorous. It can be expressed, in this instance, as a working rule: when *P. menevensis* shows some feature state intermediate between that of *C. perneri* on the one hand, and *N. americana* on the other, then the feature state in *C. perneri* is likely to represent the primitive condition from which the others were derived.

The primitiveness, or otherwise, of a feature known uniquely in *C. perneri* therefore remains undecided if its primitiveness for cornutes cannot be established in one of the following ways: 1, by outgroup comparison with echinoderms (such a comparison, if successful, would imply its existence in the crownward part of segment 1, and at least throughout segments 2, 4, 6, and 7 of text-fig. 26); 2, by its presence, perhaps in less marked form, in the least crownward of other cornutes; 3, by functional arguments. Such unique features of *C. perneri* could be primitive for cornutes (present at the junction of segments 6, 7, and 8) or could be autapomorphies of *C. perneri* evolved within segment 7. Only the recognition of stem chordates less crownward than *C. perneri*, or of nodal-group dexiothetes, will favour one or other of these alternatives. To assume that all features of *C. perneri*, even those known uniquely in it, were primitive for cornutes and existed in the chordate stem lineage, is not legitimate and leads into an intellectual trap. For it is like assuming, in view of *Ornithorhynchus*, that all other mammals evolved from a toothless ancestor, with a duck-like beak; or, in view of modern amphioxus, that the latest common ancestor of vertebrates and acraniates was brainless, which cannot be true (Jefferies 1973).

The above methodological discussion assumes the relationships which will be discussed in the rest of this section. This is legitimate, since the assignment of different cornutes to their places in the cornute cladogram does not start from a blank (see Jefferies 1979; in press, Ch. 9). Our task is to fit *P. menevensis* into a phylogenetic framework which is already partly known.

The cladogram of the dexiothetes and the position of Protocystites menevensis *within the chordate stem group*

The cladogram shown in text-fig. 26 is, in our view, the most parsimonious and probable arrangement of the Dexiothetica, so far as the facts at present available indicate. The evolutionary novelties assignable to the various segments are as follows.

Segment 1. In this segment, which was the dexiothete stem lineage, a form like the pterobranch *Cephalodiscus* lay down on its originally right side and lost the openings and tentacles of the right side and probably also the pterobranch stalk. This process of lying on the right side, with all its consequences, can be called dexiothetism. Henceforth, in the dexiothete stem lineage, the primitive and hemichordate right became ventral in chordate terms and hemichordate left became dorsal. Also a calcite skeleton of stereom mesh was acquired (Jefferies 1986, Chs. 2 and 7). No known fossil forms have yet been assigned to the dexiothete stem group through which segment 1 would have passed.

Segment 2. This is the least crownward part of the echinoderm stem lineage. The evolutionary novelties acquired in the echinoderm stem lineage as a whole (segments 2 and 4) can now be

discussed much more fully than before because of two stimulating and perspicacious recent papers (Paul and Smith 1984; Smith 1984a). In segment 2 fixation occurred, probably by extending the lower surface of the animal (corresponding to the hemichordate right side and the chordate ventral surface) down into the sea-floor. As seen from above, the mouth remained peripheral in position as in a cornute. The ambulacra leading into the mouth (presumably connected with the water vascular system and thus with the left mesocoel = left hydrocoel) became triradiate. Any gill slits on the upper surface were lost—those on the lower surface would already have disappeared as a result of dexiothetism. Thus segment 2 gave rise to the helicoplacoids as a plesion.

Segment 3. This is purely conventional, and perhaps did not exist. Three genera of helicoplacoid are known.

Segment 4. In this segment the mouth moved into the centre of the upper surface by the process known in crinoid embryology as torsion. The triradiate ambulacra became pentaradiate but retained a distinct $2+1+2$ pattern reflecting the primitive triradiality. The upper surface became flat. This produced the form *Camptostroma* which may actually lie on the echinoderm stem lineage or even be the latest common ancestor of living echinoderms (the first crown echinoderm). It thus belongs, in the present state of knowledge, to the nodal group of the echinoderms.

Segment 5 is conventional and perhaps did not exist.

All known echinoderms, apart from helicoplacoids and perhaps *Camptostroma*, are probably crown-group echinoderms, being assignable to one or other of the two primary echinoderm sub-groups (Pelmatozoa and Eleutherozoa).

The meanings of the words 'dorsal' and 'ventral' require discussion. The upper surface of pelmatozoans and stem-group echinoderms is homologous, if the above account is correct, with the left side of hemichordates and with the upper (i.e. dorsal) surface of chordates. Unfortunately, however, the use of the terms 'dorsal' and 'ventral' in echinoderm literature is based on eleutherozoans such as starfishes and sea-urchins which have inverted in evolution so that the primitive upper surface faces downwards. Hence 'dorsal' and 'ventral' in echinoderms mean the exact opposite to what they do in chordates. The chordate usage clearly has priority (Latin *dorsum* = back; *venter* = belly) and is habitual to far more people than the echinoderm usage. The best solution to this nomenclatorial difficulty would be to eliminate the words 'dorsal' and 'ventral', henceforth, from echinoderm terminology. The words 'aboral' and 'oral' have respectively the same meaning as the conventional 'dorsal' and 'ventral' in all echinoderm groups except helicoplacoids, for which the words 'upper' and 'lower' can fittingly be used with their obvious meanings.

Segments 6 and 7. A large number of important changes occurred in segment 6: the locomotory tail was acquired and reached roughly the condition seen in *Ceratocystis perneri* with fore, mid, and hind portions, while the soft parts of the tail probably included muscle blocks, notochord, and dorsal nerve cord; the brain was developed at the anterior end of the tail; the plates of the head evolved, probably to an almost rigid condition as seen in *C. perneri*; the water vascular system was lost, but the hydropore was retained as outlet for the axial sinus (which in the early embryology of crinoids it still is); the gill slits increased to seven in number (assuming that the single gill slit on the left side of *Cephalodiscus* represents the primitive complement in Dexiothetica), and probably an endostylar mucous filter developed inside the enlarged pharynx; the ear, paired trigeminal ganglia, and median eye developed; and the layout of the head chambers seen in *Ceratocystis perneri* evolved, with the viscera concentrated in the right anterior coelom to the right of the tail, and with a large pharynx, a large buccal cavity, and a posterior coelom. A virtual left anterior coelom lay dorsal to the other chambers.

Features known uniquely in *C. perneri* create special methodological problems, as already argued. Many of them were probably primitive for cornutes, i.e. were present in the crownward part of segment 6. Such include: the almost rigid surface of the head (by anti-crownward extrapolation); the presence of a single plate (w + a + x) (by anti-crownward extrapolation since plates w, a, and x are less differentiated from each other in *P. menevensis* than in '*Cothurnocystis*' *fellinensis* for

example); the large number (> 2 on either side) of dorsal segments per ventral ossicle in the hind tail (by anti-crownward extrapolation); the presence of a hydropore (by outgroup comparison with echinoderms); the position of the gonopore-anus to the right of the tail (by functional argument); the absence of a high wall in front of the brain (by functional argument since this wall is associated with the presence of the rectum in the posterior coelom, and this in turn depends on the gonopore-anus being left of the tail).

Many features known uniquely in *Ceratocystis perneri*, however, are of indeterminate status. They may have been primitive for cornutes and present in the crownward part of segment 6, or they may be autapomorphies of *C. perneri* among known forms, and in that case evolved in segment 7. Such include: the absence of an oral pyramid; the position of two of the gill slits (nos. 1 + 2) anterior to the left posterior dorsal crest; the ear penetrating plate i (it penetrates plate j in *P. menevensis*); the presence of plate o; the separation, in some specimens, of gonopore from anus; the large number of segments in the fore tail (about seventeen rings of successive plates on each side). The allocation of these features as evolutionary novelties to their correct segment must await the recognition of plesions less crownward than *C. perneri*, or perhaps between *C. perneri* and *P. menevensis*.

Segment 8. Most of the differences between *C. perneri* and *P. menevensis* probably arose as evolutionary novelties in this segment. The exceptions are features that arose in segment 7, none of which is certainly identifiable, and those that arose in segment 9 as autapomorphies of *P. menevensis*. Evolutionary novelties that probably arose in segment 8 include: loss of hydropore; migration of gonopore and anus to the left of the tail and perhaps their unification to a single opening (if this latter had not already happened in segment 6); acquisition of a high wall behind the posterior coelom, in plates g and j, forming the cerebral basin; increase in the angle between the posterior and right margins of the head (if correctly reconstructed in *P. menevensis*); reduction in the number of segments in dorsal parts of the hind tail to only slightly more than one per ossicle on either side proximally; acquisition of an oral cone (if this did not already exist in segment 6); better development of f-spike and k-spike; reduction in size of plate y.

Segment 9. Features found exclusively in *P. menevensis*, but not in *C. perneri* nor in *N. americana*, and which do not represent morphological intermediates between these two species, were probably autapomorphies of *P. menevensis*, i.e. were evolved in segment 9. Such features are minor but do seem to exist. They include: the very light build of the skeleton with two-dimensional retiform stereom in large parts of the dorsal integument and ventral floor, strengthened in the floor by irregularly placed struts to give a 'space-frame'; the roundness of the e-spike; the bluntness of the ridge on plates 1 and 2; perhaps the small number of segments in the foretail (only three, as compared with about seventeen in *C. perneri* and five in *N. americana*). The lightly built stereom strengthened by ribs, and the rounded dorsal ridges would have reduced weight and can probably be seen as adaptations to life on a very soft sea-bottom. The small number of segments in the fore tail perhaps suggests that *P. menevensis* was less motile than *C. perneri* or *N. americana*. The autapomorphies of *P. menevensis* show that segment 9 was not purely conventional but really existed.

Segment 10. Most of the differences between *N. americana* and *P. menevensis* are shared by *N. americana* with more crownward plesions and therefore arose as evolutionary novelties in segment 10. They include: the strut as a thickening of plate g in *N. americana*—as already mentioned, the strut may have begun from the internal process of plate g as seen in *P. menevensis* or by the stabilization of apposed ribs in plates g and a in the 'space-frame' structure as seen in *P. menevensis* (but in that case the space-frame type of construction would not be an autapomorphy of *P. menevensis*); the clear differentiation of anterior U-plates in the branchial slits; the breakup of plate ü into three pieces (though perhaps it was already in two pieces in *P. menevensis*); the disappearance of plates 3 and 5 as recognizable entities and the smaller size of plate 2; the fact that plate d is part of the frame instead of merely forming part of the floor of the head behind the mouth; the fact that plate 1 extends more leftwards than plate k; the accurately opposite position of left and right hind-tail plates. As already said several times, the only available specimen of *N. americana* is poor.

Segment 11. Two features of *N. americana* are unique to it and are thus likely to be autapomorphies of the species and evolved in segment 11. These are the rightward spread of the e-spike and f-spike so that both are clearly visible in dorsal aspect. These autapomorphies show that segment 11 actually existed. This is also evident on stratigraphical grounds, for *N. americana* is less crownward than the *Cothurnocystis*-like species of Sprinkle (1976), particularly in having a rigid floor to the head, but is stratigraphically later (Upper Cambrian rather than Middle Cambrian).

Segment 12. For purposes of text-fig. 26 we choose '*C.*' *fellinensis* to represent its particular plesion, mainly because Ubaghs (1969) has described this species with his usual thoroughness (text-fig. 13). Many other species of cornute belong near this position but cannot yet be accurately placed—among them the undescribed Middle Cambrian 'stylophoran' of Sprinkle (1976). Evolutionary novelties which can be ascribed to segment 12 are as follows: flexibility of the floor of the head (apart from the strut); plate t and the t-spike; and breakdown of the triple-arch of the dorsal surface so that only a line of spines anterior to the gill slits remains as a vestige. In '*C.*' *fellinensis* plate k extends somewhat further leftwards than plate l. This could be a primitive feature, in which case *N. americana* acquired the opposite condition in segment 11, or could be a secondary reversion simulating a primitive condition.

Segment 13. The only evidence for this segment is stratigraphical: '*C.*' *fellinensis* is contemporaneous with *Galliaecystis lignieresi* and *Amygdalotheca griffei* (both from the Lower Arenig of the Montagne Noire) and these two species are more crownward.

Segment 14. The chief changes in this segment are: the loss of plate y and the median eye; the loss of plate x; and the loss of the spines which in '*C.*' *fellinensis* form a curved row anterior to the gill slits. So far as can at present be determined, the family Scotiaecystidae (*Scotiaecystis*, *Thoralicystis*, and *Bohemiaecystis*) belongs to the plesion of *C. elizae*.

Segment 15. This must have existed for stratigraphical reasons. *C. elizae*, from the uppermost Ordovician (Ashgill) of Scotland is younger than all the cornute plesions crownward of it, i.e. *G. lignieresi* and *A. griffei*, both from the Lower Arenig, *Reticulocarpos hanusi* from the Llanvirn, and *R. pissotensis* from the Llandeilo. It is also younger than the earliest known members of the chordate crown group (the mitrates *Peltocystis cornuta* and *Chinianocarpos thorali* from the Lower Arenig of the Montagne Noire).

Segments 16 to 24. We shall not discuss these here since there is nothing to add to the account given by Jefferies (1986).

Thus *Protocystites menevensis* fits into a plesion between those of *Ceratocystis perneri* and *N. americana*. It increases our knowledge of the evolution of the chordate stem lineage within the less crownward cornutes.

LOCOMOTION IN *PROTOCYSTITES MENEVENSIS*

The strange shape of cornutes such as *P. menevensis* demands a functional explanation. Details of their morphology suggest that they could move rearwards, at least occasionally, pulled by the tail. Thus in *Cothurnocystis elizae* or *S. curvata* (Jefferies, in press, Ch. 7) the ventral spikes of the head have points or sharp edges anteriorly but blunt terminations posteriorly, while the anterior appendages would have sloped forwards and downwards into the mud. Both of these types of anteroposterior asymmetry would tend to prevent forward movement and to facilitate rearward movement. Also there is evidence that the tail was highly flexible in all cornutes, as is appropriate to a locomotory organ. Neither the anteroposterior asymmetry of the spikes and appendages, nor the flexibility of the tail, can be explained if the animal always rested immobile on the sea-bottom. The tail of *C. elizae* would mainly have moved from side to side, as indicated by the existence of gaps between the major plates of the fore tail on right and left but not in the ventral mid-line. Also the end part of the hind tail of *C. elizae* seems to be specially adapted for bending downwards. The

external morphology of this species therefore suggests that the animal pulled itself across the sea-floor by side-to-side wagging of the tail, gripping the sea-floor intermittently during the locomotory cycle by pushing the distal part of the hind tail downwards into the mud. The fore-tail plates of *Ceratocystis perneri* and *P. menevensis* probably likewise flexed from side to side, in view of the overlap of the fore-tail plates across the ventral mid-line. Similarly, there is evidence that the mitrates moved rearwards pulled by the tail, as suggested in particular by the presence of cuesta-shaped ribs with the steep slope of the cuestas always morphologically anterior (Jefferies 1984, 1986). An asymmetrical shape, such as the head of a boot-shaped cornute, is easier to pull across a surface than to push, since it is directionally stable when pulled but directionally unstable when pushed. This is probably the fundamental reason why cornutes and mitrates moved rearwards. With these thoughts in mind, we now reconstruct the locomotory cycle of *P. menevensis* in detail. In what follows, we use the word 'yaw' in the standard sense for rotation about a vertical axis and 'roll' for rotation about a horizontal, anteroposterior axis.

The two largest ventral spikes of *P. menevensis* are situated near the left and right ends of the head on plates k and f respectively. This suggests that movement involved yaw, with left spike and right spike acting alternately as pivots; and such a yawing motion agrees with the presumed side-to-side flexion of the tail as suggested by the ventral overlap of the fore-tail plates. The motion would have been somewhat like one way of moving a heavy cupboard across a floor, by pivoting it alternately about its left and right leading corners. The muscles moving the head of *P. menevensis* would have been mainly those filling the large lumen of the fore tail; these would have represented the motor of the animal. An adequate reconstruction of the locomoty cycle must, therefore, explain how pressure was placed alternately on left and right spikes during crawling (on the k-spike and then the f-spike, and then the k-spike again).

Our reconstruction of the locomotory cycle of *P. menevensis* is given in text-fig. 27. Text-fig. 27a shows successive stages of the cycle in dorsal aspect and in absolute space, whereas text-fig. 27b shows the head and respective positions of the tail, always in exact posterior aspect. The drawings in text-fig. 27 are based on an adjustable model where the notochord in the fore tail is represented by a flexible ruler which allows side-to-side flexion, while the head and mid and hind tail are represented by their outlines drawn on stiff white card, as described by Jefferies (1984). The dorsal projections of the mid and hind tail in text-fig. 27a have been modified according to the reconstructed inclinations of these parts in text-fig. 27b. The outline of the head is shown in dorsal aspect, neglecting the effects of inclination during roll. Ventrally prominent structures (ventral spikes, etc.) are indicated by concentrations of dots, whose density suggests the degree of ventral prominence.

Each arrow in text-fig. 27 connects a particular anatomical point in one stage with its new position in the next stage. An arrow thus indicates approximately the direction of travel, at the stage shown, of the point in question. The lengths of the arrows for the different points of a given stage also suggest their velocities relative to each other. However, successive stages shown are not supposed to be separated by equal intervals of time. The relative lengths of arrows for the same point at different stages therefore have no meaning. We have assumed that mud had strength and could resist motion, whereas water did not. The force produced by the mud on the moving tail would have been equal and opposite to the force exerted by the tail on the mud. Thus the arrows of movement are opposite in direction to the forces that the movement provoked.

At stage 1 of text-fig. 27a, b the hind tail was buried in the sea-floor and curved ventrally (by the relaxation of its dorsal muscles). This position represented the close of the previous locomotory cycle. By stage 2 the hind tail had been raised out of the mud and straightened. Between stages 1 and 2, therefore, the tip of the tail had moved upwards and a resultant downward force would have acted on the hind tail, tending to rotate the head in roll and to drive the right spike (f) into the sea-bed while lifting the left spike (k) out of the sea-bed. The actual axis of rotation of the head would have been approximately anteroposterior and probably located near the mid-ventral line of the tail attachment, which protrudes ventrally below the general ventral surface of the head. This ventral protrusion would have allowed the head to rock, see-saw fashion, alternately to right and left, resting on the protrusion and on the mid-ventral line of the fore tail.

tail buried

tail exposed

pivot

ventrally prominent areas
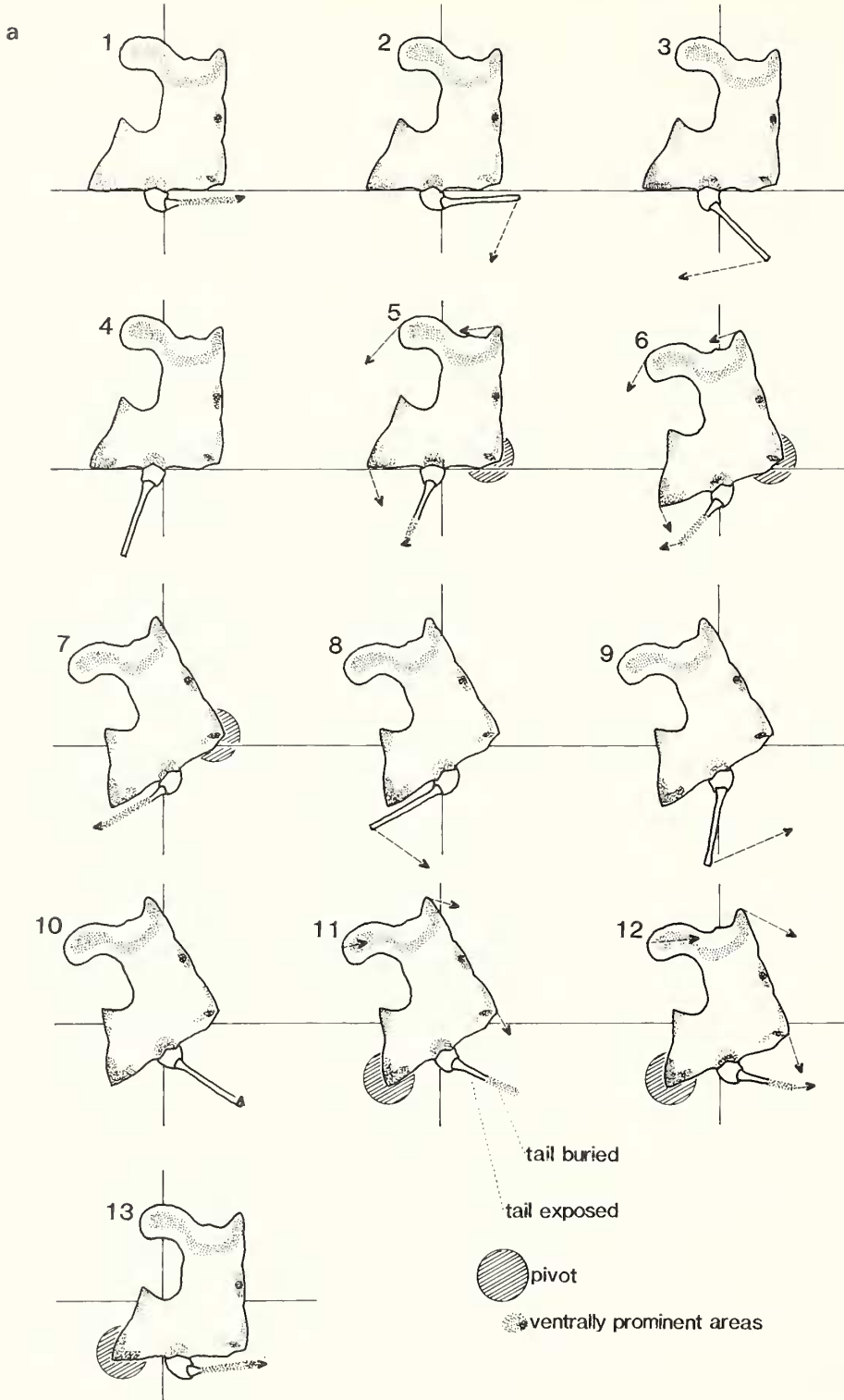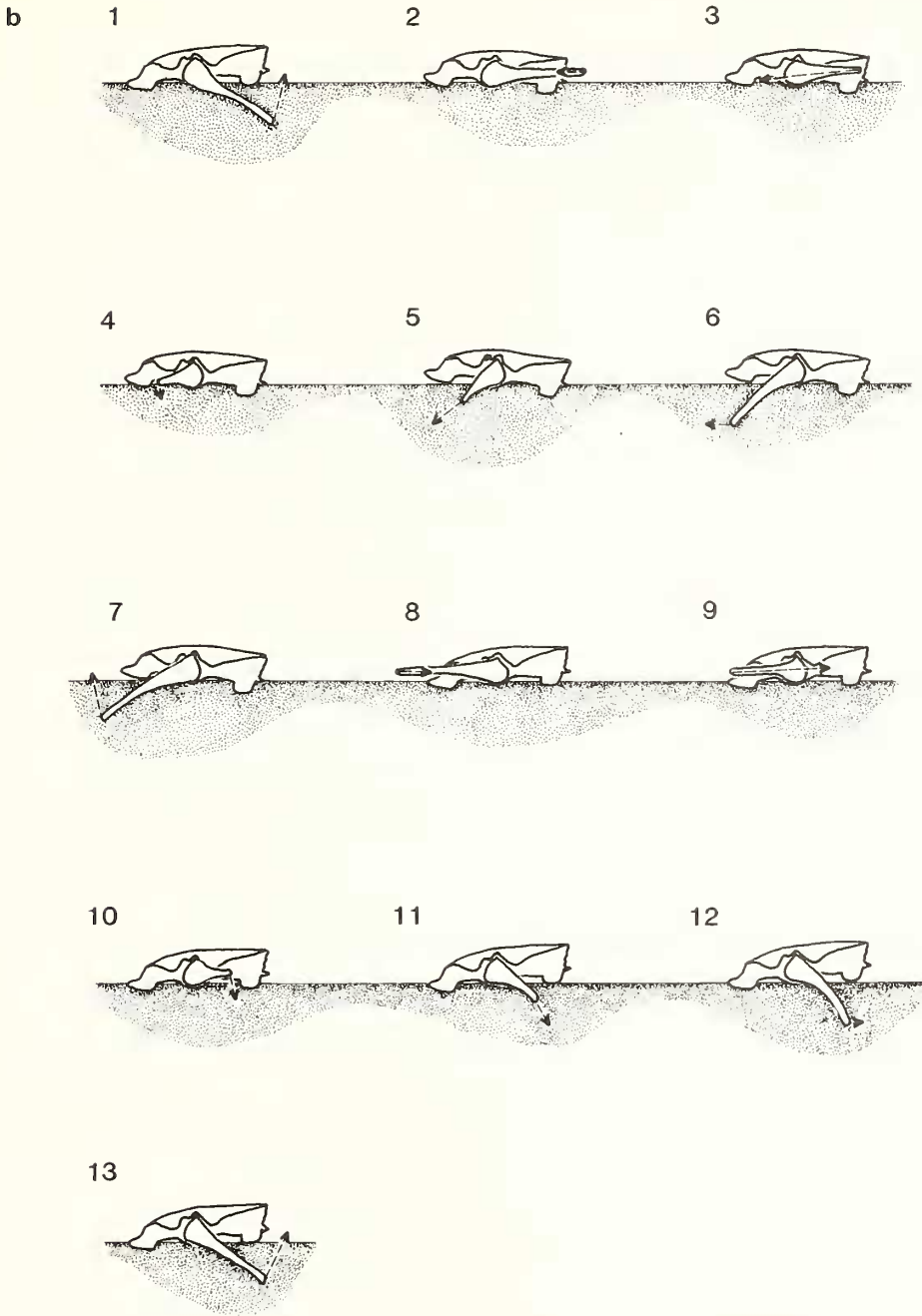
TEXT-FIG. 27. *Protocystites menevensis* Hicks; reconstructed locomotory cycle. *a*, dorsal aspect; *b*, posterior aspect (note that, unlike *a*, the viewpoint of successive diagrams is fixed relative to the animal but not in absolute space). Locomotion probably involved yaw, with the f-spike (on the right) and the k-spike (on the left) being used alternately as pivots. The head was pulled rearward by the tail when this penetrated the sea-bottom on the side farthest from the pivot. The movements of the tail in the vertical dimension, as seen in *b*, would automatically throw the weight of the head on to the intended pivot and lift the side of the head that was to be moved.

Through stages 2 to 5 the tail swung leftwards in the sea water to a position just left of the mid-line of the tail attachment. This movement, being in water, would have met little resistance and had no effect on the position of the head.

By stage 5 the hind tail had moved down into the sea-floor. This would have tended to rotate the head in roll with the same sense as previously and thus to lift the left spike further and throw the weight of the head more on to the right spike (f). At stage 6, further movement of the tail leftwards towards the head had the effect of rotating the head in yaw about the right spike as pivot. As a consequence the left side of the head moved rearwards in space. This yaw continued until stage 7.

At stage 8 the hind tail had been lifted out of the sea-floor. This movement was opposed by a force exerted by the mud downward on the hind tail which rotated the head in roll, driving the left spike down into the sea-floor and lifting the right spike. This rotation in roll was therefore opposite in sense to that between stages 1 and 2. Once again, the axis of rotation would probably have been approximately in the mid-line of the tail insertion, rocking on the ventral protrusion of the tail insertion and of the ventral mid-line of the fore tail.

Through stages 8, 9, and 10 the tail moved rightward, but in the water. The movement would therefore have met with little resistance and would have had no effect on the position of the head.

At stage 11 the mid and hind parts of the tail moved down into the sea-floor. Since these parts were right of the mid-line of the tail insertion and their movement was opposed by an upward force in the mud, the head would have tended to rotate in roll in the same sense as between stages 7 and 8, i.e. the left spike would have been driven further into the mud and the right spike lifted higher. The same rolling rotation would have tended to push the left oral appendage (b-appendage) downwards into the mud.

Through stages 11 to 13 the tail flexed rightwards and rotated the head in yaw about the left (or k-) spike as pivot. Thus the right side of the head was moved rearwards. In this yawing rotation the parts of the head furthest from the pivot would have been supported on the b-appendage (left oral appendage). This was curved approximately, though not accurately, concentric to the k-spike and therefore would scarcely have resisted the yawing rotation about that spike. At stage 13 a position was reached exactly like stage 1, except that the head had moved rearwards and rightwards. Thus the locomotory cycle was complete.

Locomotion, therefore, would probably have involved yaw alternately about the left and right spikes, combined with roll so that left and right spikes were alternately pushed into the mud and lifted clear of it. These motions of the head would have resulted automatically from the movements of the tail from side-to-side and up-and-down into the mud. The rolling movement would have been facilitated by the ventral protrusion of the head near the tail insertion. All boot-shaped cornutes, since they have spikes and appendages concentrated at left and right of the head and the same ventral protrusion of the head near the tail, probably crept rearwards somewhat in this manner.

CONCLUSIONS

P. menevensis Hicks, 1872, from the Middle Cambrian of South Wales, is a cornute and therefore a stem-group chordate. In the present paper it is described in detail for the first time and reconstructed. It shared with *N. americana* the remarkable condition that the roof of the head was flexible but the floor rigid.

Within the chordate stem group, *P. menevensis* belongs to a plesion between that of *C. perneri* and that of *N. americana*. It is crownward of *C. perneri* (i.e. more closely related to the chordate crown group) especially in lacking a hydropore, in having the gonopore-anus to the left of the tail, and in the flexible, or partly flexible, roof to the head. It is less crownward than *N. americana* especially in lacking the strut, in retaining a greater number of individualized plates in the roof of the head, and in the absence of specialized U-plates framing each gill slit anteriorly.

Specialized features (autapomorphies) of *P. menevensis* included the very lightly built stereom (particularly of the dorsal integument, of the right posterior wall of the head, and of parts of the floor of the head) and the presence of irregularly placed ribs in the lightly built parts of the floor. These autapomorphies were probably weight-saving adaptations favouring a life on very soft mud.

As to soft parts, details of the superficial internal anatomy of *P. menevensis* suggest the positions of the oesophagus, stomach, and intestine in the right anterior coelom. The left boundary of that coelom, or at least of its patent cavity, is indicated by a change in the stereom structure from retiform to almost imperforate along a line in the floor of the head.

The locomotory cycle of *P. menevensis* is reconstructed above. The animal probably crept rearwards by pivoting alternately around spikes near the left and right posterior corners of the head. This movement was produced by waving the tail alternately to the left and right while lowering it into, or raising it out of, the mud in particular parts of the cycle. This same locomotory cycle was probably usual in boot-shaped cornutes and was therefore probably primitive for stem-group chordates, so far as these are at present known.

Concerning morphological terminology, we have abandoned the objective notation of plates which was formerly used for cornutes and mitrates (e.g. Jefferies 1968). Instead we apply the comparative terminology proposed by Jefferies and Prokop (1972); this uses the same lower-case letter (a, b, é, ü, etc.) for all plates believed to be homologous in cornutes and mitrates. The terms dorsal and ventral, as conventionally used in echinoderms, should be abandoned, since in that phylum they signify the exact opposite to what they mean in chordates.

As to phylogenetic terminology, we argue that the plesion, though a useful concept in subdividing a stem group, is inherently paraphyletic when completely known, i.e. when all its constituent species are known. We use the term 'crownward' to mean 'more closely related to the crown group', with its opposites 'less crownward' to indicate phylogenetic position and 'anti-crownward' to indicate direction away from the crown group along the stem lineage. 'Crownward' is more restricted in meaning than 'advanced', for it means 'advanced along the stem lineage only'. Hennig's term 'intermediate category' is used for a paraphyletic group which provably comprises two or more adjacent plesions within a stem group. We propose the term 'nodal group' to comprise those forms which could, on the basis of synapomorphies, be crownward members of the stem group of some extant group, or could be primitive members of the crown group.

Tectonic distortion of the material made *P. menevensis* difficult to reconstruct. This distortion was corrected, to some extent, with the help of a computer program and a plotter. This correction was a necessary preliminary to the normal process of reconstructing the animal in three dimensions on a drawing board.

Thus *P. menevensis*, a strange boot-shaped animal, throws light on the evolution of our early ancestors and marks the oldest occurrence known of the chordate phylum in Britain.

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